Forest floors as affected by tree species, thinning intensity, and soil properties chemistry, element contents, and rates of turnover

Vesterdal, L.

Publication date:
1998

Document version
Publisher's PDF, also known as Version of record

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Chemistry, element contents, and rates of turnover

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Hørsholm 1998

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Contents

Abstract

The thesis explored the influence of tree species, thinning intensity, and soil properties on forest floors, i.e. the layer of dead organic matter above the mineral soil. The studies focused on forest floor characteristics such as chemistry, element contents, and rates of turnover. The objectives were to study i) if different tree species and thinning intensities affected forest floors consistently irrespective of gradients in soil properties, ii) if chemistry, element contents, and turnover rates of forest floors were related to soil properties, and iii) the influence of soil properties on decomposition through the litter quality and the soil environment.

Chemistry and element contents of forest floors differed consistently among seven tree species along a soil fertility gradient, indicating that differences among tree species in inherent litter quality affected forest floor chemistry and nutrient immobilization at both nutrient-rich and nutrient-poor soils. Microbial access to nitrogen and phosphorus in forest floors also differed among five tree species at soils of different nutrient status. The great variation in forest floor carbon content was for the most part considered to reflect differences in turnover rate, but differences in litterfall C content could not be excluded.

Thinning intensity (ranging from unthinned to 50% of unthinned basal area) influenced the chemistry and C, N, and P contents of forest floors to some extent, but the influence of thinning was not similarly strong at three different sites. Furthermore, the variation among sites of different nutrient status was greater than variation due to different thinning intensity. The differences in forest floor element contents were primarily attributed to increased rates of turnover in thinned stands resulting from a more favourable microclimate and the presence of ground flora species.

Soil properties influenced the chemistry of forest floors, and C contents were negatively related to soil fertility variables, indicating that rates of turnover increased with increasing nutrient status. Concentrations of P and Ca, pH, and soil texture were important soil fertility variables in the Danish study, whereas C and N turnover rates in forest floors were positively related to mineral soil N capital in a study in Washington, USA. There was an indication that forest floor element contents and turnover rates were less affected by soil nutrient status in some tree species than in others. Soil nutrient status affected decomposition of beech (*Fagus sylvatica* L.) leaf litter both through the quality of litter and the properties of soil environments. Decomposition of Norway spruce (*Picea abies* (L.) Karst.) needle litter was not affected by soil properties through the litter quality, and the effect of soil environment was weak. Nutrient release from litter of both species was more affected by soil nutrient status through the quality of litter than through the environmental conditions.

Forest floors may have implications for nutrition, pedological processes, regeneration, and storage of atmospheric CO_2. The order of priority for these topics determines which forest floor characteristics are considered desirable. Soil properties influenced forest floors considerably, but results in this thesis suggests that it may be possible to manage forest floors according to different objectives along extensive soil gradients by selection of different tree species and thinning intensities.

Resumé

Afhandlingen har behandlet indflydelsen af træart, hugststyrke og jordbundsegenskaber på det organiske lag i skovbevoksninger, dvs. laget af dødt plantemateriale akkumuleret ovenpå mineraljorden. Delstudierne fokuserede på det organiske lags kemiske egenskaber, mængden af akkumuleret carbon og næringsstoffer, samt omsætningen. Det var hensigten at undersøge i) om forskellige træarter og hugststyrker påvirker det organiske lag uanset variation i jordbundens næringsstofsstatus, ii) om de kemiske egenskaber, mængden af C og næringsstoffer samt omsætningen i det organiske lag kan relateres til jordbundens næringsstofstatus og iii) i hvilken grad jordbundens næringsstofstatus påvirker omsætningen via henholdsvis litteregenskaberne og jordbundsmiljøet.

Der blev fundet klare forskelle blandt syv træarter med hensyn til det organiske lags kemiske egenskaber (C/næringsstof forhold, pH) og akkumulerede mængder af C og næringsstoffer. Disse træartsforskelle gjorde sig gældende langs en betydelig gradient i jordbundens næringsstofstatus. Træartsspecifikke litteregenskaber synes dermed at have betydning for det organiske lags kemiske egenskaber og immobiliseringen af næringsstoffer på såvel næringsrige som næringsfattige jorde. Tilgængeligheden af nitrogen og fosfor for mikroorganismer i det organiske lag varierede ligeledes blandt fem træarter på jorde med forskellig næringsstofstatus. Den betydelige variation i mængden af C i det organiske lag var sandsynligvis et resultat af forskellig omsætningshastighed, selv om varierende litterproduktion hos træarterne ikke kunne udelukkes.

Hugststyrken (fra ingen tynding til 50% af utyndet grundflade) havde i nogen grad indflydelse på det organiske lags kemiske egenskaber og de ophobede mængder af C, N og P, men effekten af forskellig hugststyrke var ikke lige stor på tre jordbundstyper. Endvidere varierede mængden af ophobet C, N og P mere blandt lokaliteter med forskellig næringsstofstatus end blandt hugststyrker. Forskellig ophobning af C, N og P kan skyldes forbedret mikroklima og tilstedeværelsen af en urteflora i bevoksninger med stærk hugst.

Det organiske lags kemiske egenskaber var også relateret til jordbundsegenskaberne, og de ophobede mængder C var negativt korreleret med forskellige indikatorer for jordbundens næringsstofstatus. Dette antyder, at omsætningshastigheden var stigende med stigende næringsstofstatus. Mineraljordens P og Ca koncentrationer, pH samt tekstur var vigtige egenskaber i det danske delstudium, mens omsætningshastigheden for C og N var positivt korreleret med mineraljordens N indhold i delstudiet udført i Washington, USA. Den akkumulerede mængde C og omsætningen var dog mindre påvirket af jordbundsvariation hos nogle træarter end hos andre. Jordbundens næringsstofstatus påvirkede omsætningen af bladlitter fra bøg (*Fagus sylvatica* L.) både gennem litterens næringsstofstatus og gennem jordbundsmiljøets egenskaber. Omsætningen af nålelitter fra rødgran (*Picea abies* (L.) Karst.) var ikke påvirket af forøget næringsstofstatus i litteren, og virkningen af jordbundsmiljøet var svag. Frigivelsen af næringsstoffer fra bøge- og rødgranlitter var mere påvirket af jordbundstypen som følge af varierende næringsstofkoncentrationer i litteren end som følge af jordbundsmiljøets egenskaber.

Det organiske lag kan have betydning for næringsstoftilgængelighed,

jordbundsudvikling, foryngelse og lagring af atmosfærisk CO_2 i skovbevoksninger. Prioriteringen af disse emner i skovdriften betinger hvilke karakteristika, der vurderes som fordelagtige ved det organiske lag. Jordbundens egenskaber havde stor indflydelse på det organiske lag, men resultaterne af dette arbejde peger på, at det organiske lag kan modificeres i henhold til skovdriftens målsætninger på både næringsrige og næringsfattige jorde gennem hugststyrken og træartsvalget.

List of papers

This thesis consists of a summary part and five papers, which will be referred to by their Roman numerals

I **Vesterdal, L.** and Raulund-Rasmussen, K. Forest floor chemistry and element contents as affected by seven tree species and a soil fertility gradient. Can. J. For. Res. (submitted).

II **Vesterdal, L**., Dalsgaard, M., Felby, C., Raulund-Rasmussen, K. and Jørgensen, B.B., 1995. Effects of thinning and soil properties on accumulation of carbon, nitrogen and phosphorus in the forest floor of Norway spruce stands. For. Ecol. Manage. 77: 1-10.

III **Vesterdal, L.** Influence of soil type on mass loss and nutrient release from decomposing foliage litter of beech and Norway spruce. Can. J. For. Res. (submitted).

IV. Prescott, C.E., Chappell, H.N. and **Vesterdal, L.** Nitrogen cycling in coastal Douglas-fir forests along a gradient in soil nitrogen capital. Ecology (submitted).

V. **Vesterdal, L.** Potential microbial nitrogen and phosphorus availability in forest floors. Soil Biol. Biochem. (submitted).

Due to restrictions from the publisher of the journal in which paper II has been published, this paper is not present in this PDF. The paper can be found in:
Vesterdal, L., Dalsgaard, M., Felby, C., Raulund-Rasmussen, K., & Jørgensen, B. B. (1995). Effects of thinning and soil properties on accumulation of carbon, nitrogen and phosphorus in the forest floor of Norway spruce stands. *Forest Ecology and Management, 77*, 1-10.
DOI: 10.1016/0378-1127(95)03579-Y

Paper I, III, IV and V are present in this PDF.
Paper I and III are published in Canadian Journal of Forest Research.

The papers can be found in:
Paper I:
Vesterdal, L. & Raulund-Rasmussen, K. (1998). Forest floor chemistry under seven tree species along a soil fertility gradient. *Canadian Journal of Forest Research, 28*, 1636-1647.
DOI: 10.1139/cjfr-28-11-1636

Paper III:
Vesterdal, L. (1999). Influence of soil type on mass loss and nutrient release from decomposing foliage litter of beech and Norway spruce. *Canadian Journal of Forest Research, 29*, 95-105.
DOI: 10.1139/cjfr-29-1-95

Paper IV is published in Ecology.

The paper can be found in:
Prescott, C. E., Chappell, H. N., & Vesterdal, L. (2000). Nitrogen turnover in forest floors of coastal douglas-fir at sites differing in soil nitrogen capital. *Ecology, 81*, 1878-1886.
DOI: 10.1890/0012-9658(2000)081[1878:NTIFFO]2.0.CO;2

Paper V is published in Soil Biology & Biochemistry.
The paper can be found in:
Vesterdal, L. (1998). Potential microbial nitrogen and phosphorus availability in forest floors. *Soil Biology and Biochemistry, 30*, 2031-2041.
DOI: 10.1016/S0038-0717(98)00078-9

1 Introduction

Forest floors consist of the dead aboveground biomass deposited in a layer above the mineral soil in forest stands. The amount of accumulated organic matter in forest floors reflects the ratio between the input, i.e. the rate of litter production, and the loss, i.e. the rate of decomposition (Olson 1963). The stored organic matter contains nutrients which must be mineralized during the decomposition process in order to be available for plant uptake. The mass and nutrient contents of forest floors are very variable. In some stands, a small amount of nutrients are immobilized in organic form, while other stands may have large amounts of nutrients accumulated in the forest floor.

Forest floor characteristics and dynamics may have implications for silviculture and biogeochemical sustainability of forest ecosystems. Stands with large forest floors may have a significant proportion of the nutrient pool stored in unavailable form for the vegetation. Accumulation of large amounts of organic matter may result in increased acidity of the upper mineral soil with subsequent consequences for productivity. However, the effects of forest floor build-up on mineral soils may not be solely detrimental, e.g. increased weathering rates of soil minerals due to increased acidity might be considered positive. Deep mor-like forest floors can also be a problem for regeneration, as such forest floors are less suitable as rooting media for seedlings than the mineral soil. Lately, other aspects of forest floor carbon accumulation have attracted interest. The concern for climate change due to increasing concentrations of carbon dioxide and other greenhouse gases in the atmosphere could bring carbon binding in forest ecosystem, e.g. in the forest floor and the mineral soil, into focus. Consequently, there may be different views on organic matter storage depending on the objectives of forest management.

The first studies of forest floors were initiated because of the implications of forest floors and their morphology for silviculture. Müller (1879) described contrasting types of forest floors as they occurred in beech forests and was the first to demonstrate the relations to soil properties and soil formation. He defined mull forest floors as loose, incoherent layers of organic matter that gradually pass into the mineral soil due to intensive activity of the soil fauna. In contrast, mor forest floors were described as firm, coherent layers of organic matter with a sharp boundary to the mineral soil due to very little activity of larger soil animals. Müller (1884) also noted the influence of vegetation on humus forms in his account of humus forms under oak and *Calluna* heath. It was later recognized that vegetation considered predisposed to mor formation might develop more mull-like forest floors according to the nutrient status of the mineral soil (Hesselman 1926). The importance of both vegetation and properties of the mineral soil for forest floor characteristics was at the same time addressed in studies by Bornebusch (1923-25). Hesselman (1926) suggested that the different forest floor types were results of different decomposition rates, and in accordance, Handley (1954) concluded that it was different degradability of organic materials that caused the forest floor types rather than different rates of litter production.

Later studies have also attributed differences in element contents and decomposition rates of forest floors to soil properties (Florence and Lamb 1974, Staaf 1987,

Raulund-Rasmussen and Vejre 1995), different litter quality among tree species (Gloaguen and Touffet 1980, Aber et al. 1990, Muys et al. 1992, Johansson 1995), and climatic conditions (Fogel and Cromack 1977, Meentemeyer and Berg 1986).

Soil properties are important for the activity and diversity of decomposer species at different sites due to variation in availability of nutrients and variation in environmental conditions. For instance, fine-textured soils and soils rich in exchangeable bases may favour active, species-rich communities of decomposer organisms which comprise macrofauna species like earthworms as well as mesofauna species and microorganisms (Schaefer and Schauermann 1990, Raubuch and Beese 1995). In this way the soil type may influence the rate of organic matter decomposition and nutrient release (Herlitzius and Herlitzius 1977, Setälä et al. 1988, 1991). The quality of forest litter as a substrate for decomposer organisms is another key factor controlling the rate of decomposition. Low nutrient concentrations and high concentrations of organic polymers as phenols and lignin have been reported to hamper decomposition and nutrient release (Boerner 1984, Berg 1986, McClaugherty and Berg 1987, Nicolai 1988). Tree species exhibit great variation in these properties, but the litter quality within a single tree species may be affected by soil properties as well (Nordén 1994, Sanger et al. 1996). Thus, the soil type may influence forest floor dynamics in two ways: Through the litter quality and through the soil environment where litter decomposition takes place. Coniferous tree species have often been reported to have a less favourable litter quality than broadleaves (Cole and Rapp 1981, Vogt et al. 1986), but this conclusion could be confounded with the influence of soil type, as conifer species are often found naturally or cultivated on poorer soils than broadleaves. At a regional scale, climatic variation also influences decomposition. Increasing temperatures may enhance the activity of decomposers, but moisture conditions must be sufficient at the same time (Howard and Howard 1979, Orchard and Cook 1983, Virzo de Santo et al. 1993, Martin et al. 1997). Within stands of the same species, the microclimatic conditions may be changed in favour of decomposer organisms by the thinning intensity. Increasing thinning intensity may lead to increased thermal and solar radiation and reduced evapotranspiration (Aussenac 1987) thereby increasing temperatures and moisture. It has also been suggested that thinning increases litter nutrient status. This was attributed to reduced competition for nutrients by the roots of the trees remaining after thinning (Carlyle 1995, Hökkä et al. 1996). Increased numbers of earthworms and other soil fauna species were also reported as a result of thinning (Bornebusch 1933, Scohy et al. 1984), possibly due to development of a herbaceous ground flora and due to improved moisture conditions. These effects of thinning may influence the decomposition rate positively (Piene and Van Cleve 1978, Kim et al. 1996) and lead to a decreased forest floor mass (Wollum and Schubert 1975, Carey et al. 1982). However, no effect of thinning intensity was also reported by Will et al. (1983). The possible influences of tree species, thinning intensity, and soil properties are summarized in Fig. 1.

Some of the above-mentioned factors (e.g. soil and macroclimate) are permanently associated with a site and cannot be modified by forest management to any great extent. However, tree species is a factor which may be modified, and the stand climate may possibly

be managed by thinning operations as well. The question remains, to what extent can forest floors be managed by the selection of tree species and by the thinning intensity while the "fixed" factors also influence forest floor characteristics? For instance, the effect of changing tree species or of increased thinning intensity might not be strong enough to result in faster turnover at soil types predisposed to pronounced accumulation of forest floor organic matter.

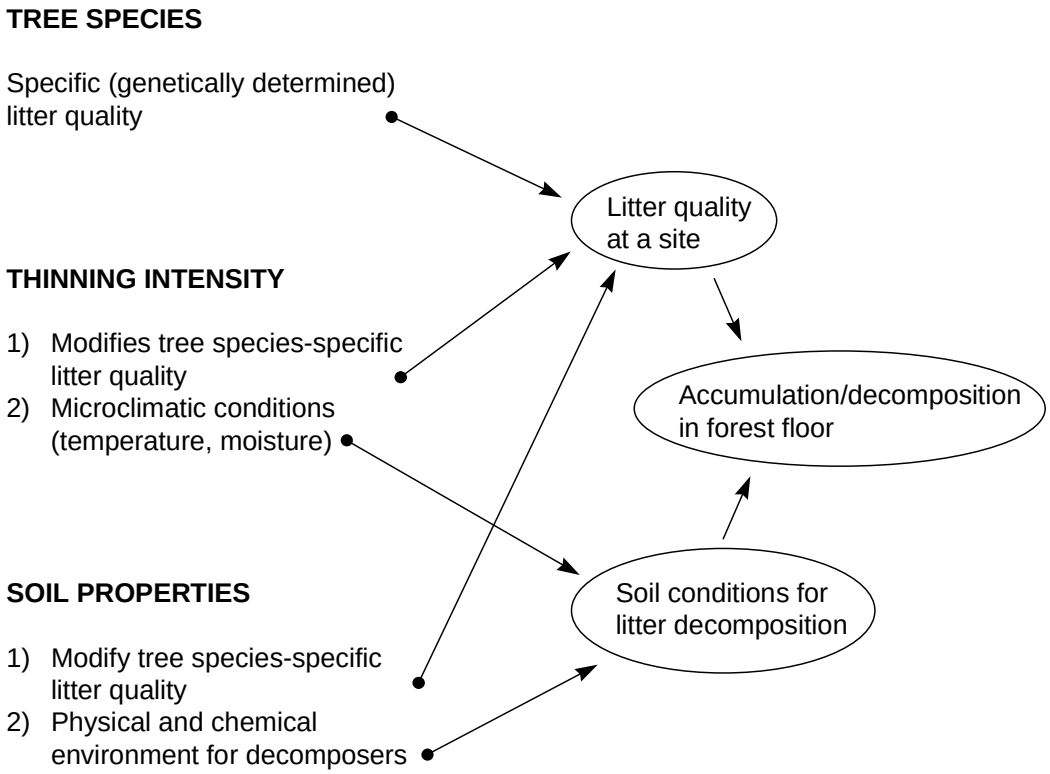

Fig. 1. Possible effects of tree species, thinning intensity, and soil type on accumulation and decomposition of organic matter in forest floors.

2 Objectives

The objectives were to explore the effects of tree species and thinning intensity on forest floors at sites that differed widely in nutrient status, and to examine the influence of soil properties. Focus was on quality and quantity aspects of forest floors, i.e. chemistry and stored amounts of elements, but rates of turnover and nutrient release were also studied.

The following hypotheses were addressed:

- Tree species affect the chemistry, element contents, and turnover rate of forest floors along gradients in soil nutrient status.
- The thinning intensity influences i) the chemistry of forest floors and ii) the accumulation of carbon and nutrients in forest floors at different soil types.
- Soil nutrient status affects forest floor chemistry, element contents, and turnover rate.
- Soil types influence decomposition and nutrient release i) by modifying the inherent litter quality of a tree species and ii) by offering different physical and chemical

conditions which affect the activity of decomposer organisms.

Effects of tree species have often been studied within single sites or at very few sites which also differed in other site properties than soil nutrient status. As the soil type influences forest floors as well, this has made it difficult to conclude whether an effect of tree species was independent of soil type. Forest floors of different tree species might respond differently to variation in soil nutrient status, e.g. the difference among species could be greater at nutrient-rich soils than at nutrient-poor soils. Soil nutrient status varies greatly within a small geographic area in Denmark, and the topography is flat. This provides an excellent opportunity of examining effects of tree species and thinning intensity in combination with effects of soil properties within a fairly similar climatic regime.

Paper I focused on the effect of tree species on forest floor chemistry and element contents along an extensive gradient in soil nutrient status. Forest floors were sampled on an area basis and were chemically analysed. Forest floor chemistry and C content were related to soil nutrient status.

Within stands of the same tree species, thinning operations may be a means of increasing the forest floor turnover rate by creating a more favourable microclimate. **Paper II** presents the effects of different thinning intensities on chemistry and C, N, and P contents of Norway spruce forest floors sampled on an area basis. The studied thinning intensities ranged from unthinned stands to stands with 50% of unthinned basal area. The effects of thinning were studied at three sites with different soil properties in order to examine whether an effect may be achieved at sites with different soil nutrient status.

The influence of soil properties on decomposition and forest floor element contents may be associated with variation in litter quality and with variation in the environmental conditions for decomposer organisms. In **paper III** the influence of soil type on decomposition and nutrient release was partitioned into an effect of soil-mediated litter quality and an effect of incubation environment for beech and Norway spruce litter using the litterbag technique.

Nitrogen is an important growth limiting nutrient in many forest ecosystems, and cycling and availability of N are therefore essential ecosystem characteristics. It is generally considered that rates of nitrogen turnover are more rapid on sites with inherent high availability of N than on sites poor in nitrogen, but this concept is mainly based on studies including different tree species. In **paper IV** it was explored whether N turnover rate and N availability in forest floors increase with increasing soil N capital within stands of a single tree species. Nitrogen turnover rates were estimated from the ratio between litterfall N content and forest floor N content.

Chemical analyses of forest floors by extraction or digestion methods as in papers I and II may not be the best parameters in relation to biological activity in forest floors. **Paper V** presents the results from a bioassay using respiration rate response in order to characterize the microbial availability of nitrogen and phosphorus in forest floors of five different tree species.

Manipulation of soil nutrient status, e.g. by fertilization and liming, was not included in

this thesis, but the short-term and long-term effects on nutrient mineralization and turnover rates were considered in other studies (Vesterdal and Raulund-Rasmussen in prep., Chappell et al. 1997).

3 Materials and methods

3.1 Tree species and sites

The studies concentrated on forest floors in monoculture stands of seven tree species: The conifers Norway spruce (*Picea abies* (L.) Karst.), Sitka spruce (*Picea sitchensis* (Bong.) Carr.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis* Lindl.), and lodgepole pine (*Pinus contorta* Dougl.) and the broadleaves beech (*Fagus sylvatica* L.) and common oak (*Quercus robur* L.). Effects of tree species and soil properties (papers I, III and V) were studied in a tree species trial with even aged stands of the above-mentioned tree species replicated in a regular design at sites with different soil nutrient status (Holmsgaard and Bang 1977). The influence of thinning intensity (paper II) was studied in a permanent thinning trial in Norway spruce replicated at three nutritionally different sites. Nitrogen cycling within a single tree species (paper IV) was examined in nine Douglas-fir stands along a gradient in soil N capital in coastal Washington and Oregon, USA.

3.2 Sampling of forest floors and litterfall

Forest floors were sampled randomly for chemical analysis and determination of element content (papers I, II, IV). Forest floors were collected on an area basis (ten 25x25 cm samples (papers I and II) or five 30x30 cm samples (paper IV) per stand). All forest floor subhorizons were pooled (papers I and IV) or were divided into a litter layer and a fermentation/humus layer fraction during sampling (paper II). For the respiration rate bioassay (paper V), newly shed litter was removed, and only partially decomposed forest floor material was sampled. Care was taken not to include mineral soil and to remove twigs, cones/fruits, roots, moss and any other vegetation. Litterfall (paper IV) was collected bimonthly during a year using ten 0.135 m^2 plastic trays with fiberglass screen in the bottom.

3.3 Litterbag technique

Decomposition of beech and Norway spruce foliage litter as affected by soil type was studied in an experiment using reciprocal transplantation of litterbags (paper III). The beech and Norway spruce litter was collected in adjacent stands at three sites of different nutrient status and was enclosed in polyester net bags measuring 13 x 15 cm with a mesh size of 1 mm^2. Litter from the three sites were incubated in stands of the respective tree species at each of the three sites in order to examine the effect of different litter qualities and the effect of different incubation environments due to variation in soil nutrient status. The litterbags were fastened to the forest floor according to a randomized block design (Johansson 1994). Litterbags were collected twice a year during 2.5 years. Concentrations of nutrients, lignin, and water and ethanol extractable substances were determined in the fresh litter. Mass and nutrient

concentrations in residual foliage litter were determined at each collection.

3.4 Respiration rate bioassay

The bioassay for potential microbial N and P availability (paper V) used respiration rate as response to addition of glucose together with N and P in different doses (Nordgren 1992). Respiration rate was measured at 20°C by a conductometric method in which evolved CO_2 was captured by a potassium hydroxide solution (Nordgren 1988). The conductivity of the solution was measured hourly, and the decrease in conductivity was converted automatically to respiration rates.

3.5 Methodological considerations in relation to turnover rate estimates

The forest floor turnover rate expresses how fast litter is decomposed. Decomposition of organic matter and the contemporary mineralization of incorporated nutrients were studied by use of more or less direct methods. For instance, the forest floor C content may serve as a rough indicator of forest floor C turnover rate. However, this does not take into account that the forest floor C content reflects a dynamic equilibrium between the rate of litter C production and the rate of C turnover. Consequently, true relative estimates of turnover rate are only provided by forest floor C content in case of similar litterfall C contents among the compared stands. In paper II litterfall C was assumed to be fairly similar among thinning treatments and sites based on comparable stem volume increments (Miller 1984). Also, it was considered unlikely in paper I that greater litterfall C content was responsible for larger C accumulation at nutrient-poor sites than at nutrient-rich sites. In such cases, forest floor C contents may provide an indication of turnover rate differences. In contrast, it is more difficult to deduce turnover rate differences among tree species from C accumulation (paper I), as tree species with very different stem volume production might differ significantly in litter production.

A better indication of turnover rate differences may consequently be obtained by relating the accumulated amounts of C to the annual litterfall C content. This estimate of turnover rate, the litterfall/forest floor ratio (LF/FF ratio), may be calculated with the following formula according to Olson (1963).

$$k = L/X_{ss}$$

where k is the turnover rate constant, L is the annual litterfall and X_{ss} is the amount of organic matter accumulated in the forest floor at the soil surface. This ratio expresses the proportion of the forest floor mass decomposed annually, as it is assumed that stands have reached steady state, i.e. that annual litter production equals the amount of forest floor decomposed per year. Litterfall should ideally be continuously distributed though the year. This method takes into account that rates of turnover may differ between stands with the same forest floor mass if rates of litter production are different. Turnover rates for C and N were estimated by this method in paper IV by relating litterfall element content to forest floor element contents.

Drawbacks of the method are that it may, in fact, indicate the rate of disappearance from forest floors rather than the decomposition rate. The incorporation of forest floor material into the mineral soil may be appreciable at sites with litter-burrowing macrofauna species. Further, the method does not enable studies of specific litter samples during decomposition.

The most direct indication of turnover rate differences may be obtained with the litterbag technique which was used in paper III. This method follows specific samples of litter and enables studies of dynamics in mass loss and nutrient release. On the other hand, this method has a drawback compared to the LF/FF ratio method due to the confinement of litter in net bags. The microenvironment may be different inside the litterbags (e.g. moisture conditions), and macrofauna species are often excluded by a small mesh size (Johansson 1986).

4 Results and discussion

4.1 Tree species

4.1.1 Forest floor chemistry

The chemistry of forest floors was clearly related to tree species, and there were distinct differences along an extensive gradient in soil nutrient status (paper I). The most acid forest floors were found in lodgepole pine, Sitka spruce, oak, and Douglas-fir. Lodgepole pine, and to some extent also Sitka spruce, tended to have the highest forest floor C/nutrient ratios, whereas oak, beech, grand fir, and Norway spruce were richer in P, Ca, Mg, and K in proportion to C. The influence of tree species was consistent although properties of the mineral soil varied greatly. This suggests that inherent differences in litter quality among tree species was an important factor for the quality of forest floors. In paper III, litter of beech and Norway spruce was collected at three of the seven sites included in paper I. The quality of spruce litter tended to be less favourable than the quality of beech litter at the three nutritionally different sites (lower nutrient and higher lignin concentrations). Accordingly, forest floor C/Ca, C/Mg, and C/K ratios were slightly, but not significantly, higher for spruce than for beech. The chemistry of forest floors may be a result of both litter chemistry and nutrient dynamics during the decomposition process.

The variation in forest floor chemistry indicated that tree species may offer different conditions for decomposer organisms. While forest floors were characterized in paper I by use of traditional chemical analyses, the microbial N and P availability in forest floors was assessed in a bioassay in paper V. Total analysis and extraction analysis are often used to describe the quality of organic matter for decomposer organisms by means of certain indicator parameters. However, these parameters do not necessarily provide information about nutrient availability to microorganisms. The purpose of the bioassay was to gain information about N and P availability from a functional point of view. Among five tree species (oak, beech, Sitka spruce, Norway spruce, and Douglas-fir), forest floors of oak had the highest microbial N and P availability. Norway spruce forest floors had the lowest N and P availability, but did not differ much from Sitka spruce, Douglas-fir and beech. The bioassay results were consistent with the result in paper I that oak forest floors had a relatively favourable P status, but the

differences in microbial N and P availability between oak and the other tree species were much greater than indicated by differences in C/N and C/P ratios in paper I. Apparently, other factors than total N and P concentrations were also important for the microbial access to N and P. The microbially available N and P fractions explained differences in basal respiration rate better than the traditional indices of N and P status in paper I, i.e. C/N and C/P ratios. This suggests that total amounts of N and P might not be the only important factors for microbial activity. The forms of N and P, especially the degree of N immobilization due to reactions with polyphenols (Kelley and Stevenson 1995), might be a contributing factor as well.

4.1.2 Forest floor element contents and turnover rate

Forest floors of seven tree species replicated at seven sites had very different contents of C, N, P, Ca, Mg, and K (paper I), i.e. the tree species affected nutrient immobilization differently along an extensive soil fertility gradient. Lodgepole pine forest floors, exhibiting the highest C/nutrient ratios and the lowest pH values, also accumulated the largest amounts of C, N, and P. Oak and grand fir accumulated the smallest amounts of C and nutrients. Inherent tree species properties were thus also important for element storage irrespective of soil nutrient status. These results support the general belief in influence of tree species achieved in studies conducted at single soil types or at soil types of more similar nutrient status (Gloaguen and Touffet 1980, Alban 1982, France et al. 1989, Son and Gower 1992, Eriksson and Rosén 1994).

An indication of turnover rate differences may be deduced from the variable C contents, if litterfall rates were comparable among tree species. Litterfall rates were not available for all 49 stands, but Miller (1984) found that foliage litterfall could be expressed as a function of stem volume increment for different tree species along a boreal-tropical climate gradient. The deciduous tree species had lower stem volume increment than the conifer species, and litterfall rates could therefore have been lower too. Table 1 shows average C contents in foliage litterfall for seven stands of each tree species derived from stem volume increment during 10 years according to the relationship proposed by Miller (1984). Turnover rate estimates were subsequently calculated by the LF/FF ratio method using the derived litterfall rates. Reservations have to be made concerning the assumptions about steady state and continuous litterfall. Due to relatively low stem volume increment at all sites, derived rates of litterfall were distinctly lower for oak and beech than for conifers. Beech and oak were consequently ranked lower in turnover rates than expected from forest floor C contents, while the highest turnover rates were estimated for grand fir due to low forest floor C contents in combination with high stem volume increment. The large C contents of lodgepole pine forest floors suggested this species had slow turnover, and this was supported by the turnover rate estimate. Turnover rates were also estimated by the LF/FF ratio method in five tree species at Ulborg (nutrient-poor site) and Frederiksborg (nutrient-rich site) using available litterfall data (Table 1). The litterfall C contents derived from stem volume increment appear too high for the conifers compared with measured litterfall C content, while derived litterfall C content for

the less productive species oak tends to be too low. The two litterfall estimates for beech were more in keeping with each other. Thus, the litterfall measurements suggested less variation among tree species in foliage litterfall C content. Deviations in litterfall estimates were most critical for turnover rate calculation at Frederiksborg due to the low forest floor C contents. Turnover rates based on measured litterfall were consequently lower for the conifers and higher for oak than turnover rates based on derived litterfall. Forest floor C content appeared to be more variable among tree species than measured litterfall C content. For these seven tree species, forest floor C contents may provide a reasonable indication of differences in turnover rate.

Table 1 also shows turnover rates based on a 2.5-year litterbag study with native litter incubated in beech and Norway spruce stands at three of the seven sites (paper III). The litterbag study revealed only small differences in turnover rate for beech and Norway spruce litter, and differences in turnover rate were not in keeping with differences in C accumulation between tree species at all three sites. Beech litter decomposed faster than spruce litter at Løvenholm, but the inverse pattern was found at Ulborg. Differences between beech and spruce turnover rates in litterbags were thus not consistent among the three sites.

Table 1. Average C content of forest floors of seven tree species and turnover rates based on increment-derived C content in foliage litterfall. Turnover rates based on increment-derived litterfall are also shown for selected tree species at four of the seven sites for comparison with turnover rates based on measured litterfall and turnover rates based on the litterbag technique.

	C content (Mg ha^{-1})	Derived[1] litterfall C (Mg ha^{-1} yr^{-1})	Turnover rate (yr^{-1})	Measured[2] litterfall C (Mg ha^{-1} yr^{-1})	Turnover rate (yr^{-1})	Litterbag Turnover rate[3] (yr^{-1})
Average of 7 sites						
Oak	2.94	0.84	0.66			
Grand fir	5.81	2.93	0.97			
Beech	7.25	1.09	0.29			
Douglas-fir	8.07	2.32	0.44			
Norway spruce	11.09	2.42	0.31			
Sitka spruce	11.25	2.78	0.31			
Lodgepole pine	17.31	1.84	0.11			
Ulborg						
Oak	6.10	0.47	0.08	1.21	0.20	
Beech	19.26	0.76	0.04	1.09	0.06	0.23
Douglas-fir	15.92	2.10	0.13	0.88	0.06	
Norway spruce	19.78	1.44	0.07	0.98	0.05	0.27
Sitka spruce	20.69	2.49	0.12	1.82	0.09	
Frederiksborg						
Oak	1.51	1.10	0.73	1.77	1.17	
Beech	2.92	1.43	0.49	1.41	0.48	
Douglas-fir	2.34	2.76	1.18	0.90	0.38	
Norway spruce	4.54	2.75	0.61	1.49	0.33	
Sitka spruce	7.21	3.00	0.42	1.80	0.25	
Christianssæde						
Beech	2.57	1.32	0.51			0.32
Norway spruce	6.33	2.84	0.45			0.30
Løvenholm						
Beech	3.50	1.07	0.30			0.40
Norway spruce	5.97	2.41	0.40			0.28

[1] foliage litterfall = (stem volume increment)*0.178 + 0.173 (model based on data used by Miller (1984)).
Carbon concentration estimated at 50%.

[2] J. Bille-Hansen, Danish Forest and Landscape Research Institute, unpublished data.

[3] Turnover rates for a 2.5 year period estimated using a negative exponential model $X/X_0 = e^{-kt}$, where X/X_0 is fraction mass remaining at time t (years), and k is the decomposition rate constant (Olson 1963). Decomposition in litterbags followed a first order kinetics in all six stands ($p < 0.001$).

4.2 Thinning intensity

4.2.1 Forest floor chemistry

Forest floor chemistry differed only little along a gradient in thinning intensity (paper II), but C/N and C/P ratios tended to be lowest in some of the strongly thinned stands, whereas pH tended to be highest in these stands. A more favourable forest floor chemistry in thinned stands may be due to a more nutrient-rich litter, as competition for nutrients among the remaining trees is reduced. This effect of thinning have been reported from other studies (Carlyle 1995, Hökkä et al. 1996). However, it was also noted that increased thinning intensity led to development of a ground flora, which could enrich forest floors through production of nutrient-rich litter. The ground flora developing as a consequence of thinning was most vigorous and rich in herbs at the nutrient-rich site, whereas grasses dominated the ground flora at the most nutrient-poor site. In conclusion, the effect of thinning on forest floor chemistry appeared to be limited compared with the difference in chemistry among sites.

4.2.2 Forest floor C, N, and P contents

The C and P contents of forest floors were negatively related to thinning intensity, and the correlation between N content and thinning intensity was nearly significant too. Carbon, N, and P contents tended to be differently affected by thinning at the three investigated sites. The strongest influence of thinning was found at the nutrient-rich site with little C, N, and P accumulation, whereas the effect of thinning appeared to be obscured by other site-specific factors at the most nutrient-poor site with the greatest C, N, and P accumulation. The variation between thinning treatments within sites was much smaller than the variation between sites, suggesting that C, N, and P contents of forest floors may be managed only to some extent by thinning intensity. The different forest floor C contents were for the most part attributed to different turnover rates, as litterfall rates probably were comparable considering that annual increment was approximately the same (Miller 1984). In detail, however, needle litter production could be lower in the strongly thinned stands because of decreased canopy closure at times, and there might also be a smaller input of root litter, as the root mass in forest floors decreased with increasing thinning intensity. The limited influence of thinning intensity on forest floor chemistry could indicate that faster turnover was caused by a more favourable microclimate (Aussenac 1987) rather than by an effect of thinning on litter quality. The ground flora in thinned stands may also have a positive effect on the turnover rate. Mixing of the Norway spruce litter with more favourable substrates for decomposer organisms might increase the species diversity and activity, and consequently lead to faster turnover (Chapman et al. 1988, Taylor et al. 1989). A more herb-rich ground flora in strongly thinned stands at the rich site might contribute to faster turnover than at the more poor sites with grass-dominated ground floras.

4.3 Soil properties

4.3.1 Forest floor chemistry

Forest floors differed in chemistry along gradients in soil nutrient status (papers I and II). pH,

C/P, C/Ca, and C/K ratios in forest floors were related to pH, and concentrations of P, Ca, and K, respectively, in the mineral soil (paper I). Increasing soil pH was associated with increasing forest floor pH, and increasing soil nutrient status was associated with decreasing C/nutrient ratios in forest floors. These relationships were found for seven tree species, and indicated that soil nutrient status affected forest floor quality variables positively, probably owing to an effect of soil nutrient status on litter quality. The litter quality of beech and Norway spruce varied considerably with respect to nutrient concentrations at three sites covering the same gradient in soil nutrient status (paper III). Nutrient concentrations were for the most part related to soil nutrient status. In Washington, USA, N concentrations in Douglas-fir needle litter were also positively related to mineral soil N capital (paper IV). In contrast, N concentrations in the American forest floors were negatively related to mineral soil N capital implying that forest floor N concentrations not always reflect litter N concentrations. Vegetation at N-poor sites may produce litter with a higher amount of phenolics than vegetation at N rich sites (Gosz 1981, Flanagan and Van Cleve 1983). Low C/N ratios in forest floors on N-poor soils may consequently also be related to reactions between amino-N and phenolics (Fog 1988; Kelley and Stevenson 1995), resulting in higher N retention in forest floors and lower C/N ratios. Consequently, C/N ratios may not be the most appropriate indicator of N availability. Accordingly, the bioassay for microbial N availability did not correspond with differences in C/N ratios among sites (paper V). Microbially available N and respiration rates tended to be lowest at the site with lowest forest floor C/N ratios. Again, this questions the general applicability of forest floor C/N ratios as predictors of microbial activity. Microbial P availability to some extent reflected soil P status and forest floor C/P ratios. The bioassay indices for N and P availability explained the variation in respiration rate better than KCl extractable N, C/N ratios or C/P ratios. This leads to the conclusion that bioassays for nutrient availability may provide better indications of factors limiting rates of turnover in forest floors at different soil types.

The root mass in Norway spruce forest floors increased considerably from a nutrient-rich to a relatively nutrient-poor soil. This occurred both within unthinned and strongly thinned stands (paper II). Gadgil and Gadgil (1971, 1975) proposed that roots associated with mycorrhizal fungi were able to compete effectively with free-living saprophytic microorganisms for nutrients in forest floors, thereby suppressing overall turnover rates. This hypothesis was not supported by Zhu and Ehrenfeld (1996), in fact mycorrhizal roots were found to stimulate mass loss and roots did not withdraw nutrients directly from litter. Nevertheless, the pattern in C/P ratios in litter and humus layers of the forest floors in paper II prompted speculation whether roots influenced the conditions for saprophytic organisms. C/P ratios were consistently highest in the litter layer at the two most nutrient-rich sites, and this pattern was attributed to microbial immobilization of P during decomposition as also observed in the litterbag study (paper III). In spite of high C/P ratios in the litter layer at the nutrient-poor site (600-700), C/P ratios were significantly higher in the humus layer indicating that P should be mineralized faster than C. This appeared unlikely with such high C/P ratios (Harrison 1987) but the relative decrease in P might have been caused by selective

decomposition or extraction of P by mycorrhizal roots. In the light of the large root mass in forest floors at this relatively poor site and reports that mycorrhizae produce specific enzymes for P mineralization (Häussling and Marschner 1989; Dighton 1991), this could provide an explanation for the pattern in C/P ratios.

C/N ratios were consistently highest in the litter layers at all three sites, suggesting that N was retained longer than C during decomposition as in the litterbag study (paper III). Thus, there was no indication of selective N extraction at any of the three sites.

4.3.2 Forest floor element contents, turnover rate, and nutrient release

Forest floor element contents varied considerably along gradients in soil nutrient status (papers I and II). Carbon accumulation in the forest floor was negatively related to mineral soil fertility variables such as P and Ca concentrations, pH, and fineness of soil texture (paper I), thereby supporting the hypothesis that soil nutrient status affects accumulation of C and nutrients in forest floors. However, forest floors of oak and lodgepole pine tended to deviate from this pattern. Lodgepole pine forest floors had the highest C content of all species, and the C content did not decrease with e.g. increasing soil P and Ca concentrations. Oak forest floors had the lowest C content, and it increased less than C contents of beech, grand fir, Douglas-fir, Norway spruce, and Sitka spruce with decreasing soil nutrient status. It was suggested that less C accumulation at nutrient-rich sites could be interpreted as faster turnover since litterfall would be expected to increase with increasing soil fertility rather than the opposite. This expectation was supported by litterfall C content measured at two of the sites with very different nutrient status (Table 1). However, inputs of root litter could be highest at the nutrient-poor sites (paper II).

Soil N concentration was in paper I unexpectedly found to be positively related to forest floor C content, but the positive correlation was presumably a result of high N concentrations in soils that were poor in other nutrients. In contrast, paper IV reported that forest floor C content in Douglas-fir forests in Washington tended to be negatively related to soil N capital (Mg N ha^{-1}), and forest floor N content was significantly negatively related to soil N capital. The positive correlations between soil N capital and rates of C and N turnover were even stronger, and rates of turnover were also negatively related to C/N ratio in the mineral soil. Contrary to the Danish study (paper I), there were no significant relationships between C accumulation or C turnover rate and other soil fertility variables than N capital in the Douglas-fir forests in Washington. However, there was an indication that soil texture could be of some influence too. This difference between studies probably reflects that soils in Washington were rich in P, and that gradients in pH and exchangeable bases were smaller and less important than the N gradient. C/N ratios in litterfall and forest floors varied more in Washington, and the level of C/N ratios indicated that N status was lower than in Denmark. Papers I and IV both lead to the conclusion that soil nutrient status may affect forest floor element contents and element cycling, although the characteristics of soil gradients were different.

It was hypothesized that this effect of soil nutrient status on organic matter accumulation

and turnover rate in forest floors could be due to i) litter quality differences as also indicated by the variable chemistry of forest floors, and ii) differences in the soil environment affecting the activity of decomposers. These effects of soil nutrient status on decomposition were studied in two tree species by separating the effects of soil type into an effect of soil type-mediated litter quality and an effect of the soil environment (litterbag incubation site) (paper III). Decomposition of beech litter was positively affected by soil-mediated litter quality, whereas there was no effect of varying nutrient status in litter of Norway spruce. Decomposition was positively affected by incubation site nutrient status in both tree species, but the effect was weak for spruce litter. These differences between beech and Norway spruce decomposition led to the same conclusion as in paper I that C storage and turnover rate in different tree species may be variably affected by soil nutrient status. The litter quality, e.g. the concentrations of recalcitrant compounds, could be so unfavourable in tree species like Norway spruce and lodgepole pine that increased nutrient concentrations are insufficient for microorganisms to decompose faster.

Nutrient release from the decomposing beech and Norway spruce litter did not solely reflect mass loss. The influence of soil type on nutrient release was primarily due to the effect of soil type on litter nutrient concentrations (paper III). The nutrient status of litterbag incubation sites had little or no effect, and nutrient release was not consistently related to the soil nutrient status at the sites. The soil type probably affects nutrient release more through the litter quality than through the physical and chemical conditions offered for decomposers when nutrient release is not limited by physical breakdown of litter. However, it is possible that the influence of soil-induced litter quality on nutrient release decreases during later stages of decomposition, whereas the importance of the soil environment may increase (McClaugherty et al. 1985). Sites with inherent high availability of nutrients are often believed to have fast nutrient cycling. Gosz (1981) hypothesized that forests at N-rich sites produce N-rich litter leading to rapid decomposition and mineralization of N, while forests at N-poor sites produce N-poor litter which decomposes slowly and releases the N slowly. The study in paper IV tested the hypothesis that this positive feedback would also apply within a single tree species, and found that rates of N turnover in forest floors increased with increasing soil N capital.

Turnover rate estimates based on the LF/FF ratio using measured or derived litterfall C contents and turnover rate estimates based on the litterbag technique did not correspond equally well among soil types (Table 1). Litterbag turnover rate estimates corresponded reasonably well with LF/FF ratio turnover rates at Løvenholm, but litterbag estimates were lower at Christianssæde and much higher at Ulborg than LF/FF ratio turnover rates. Lower estimates of turnover rate with the litterbag technique at Christianssæde may be due to exclusion of macrofauna species, e.g. earthworms, which may speed up decomposition and burrow forest floor material in the mineral soil (Stout 1983). Johansson (1986) reported that the litterbag technique tended to underestimate turnover rates at nutrient-rich sites inhabited by macrofauna species compared with the LF/FF ratio method. The higher LF/FF ratio turnover rate may therefore partly result from inclusion of macrofauna activity in this estimate. This may in fact lead to overestimation of forest floor turnover rates at rich sites, as burrowing

of litter in the mineral soil does not imply that the litter is decomposed at the same time. Too high estimates may also have been achieved with the LF/FF ratio method, if the stands were not approaching steady state yet. However, using the litterbag turnover rate estimates (*k*), 95% of steady state would be attained after approximately 10 years (3/*k)* at Christianssæde (Olson 1963). The large difference between litterbag and LF/FF ratio turnover rate estimates at the poor site Ulborg emphasizes how turnover rate estimates may differ between a method which measures early-stage decomposition (litterbags) and a method which integrates the whole decomposition process. The results suggest that turnover rates are not constant at Ulborg through all stages of decomposition, as in a negative exponential model. Decreasing turnover rates with time were also found by Johansson (1986) for Scots pine (*Pinus sylvestris* L.) needle litter. Turnover rates could therefore be highly overestimated if only early-stage decomposition is considered. Another reason for lower turnover estimates with the LF/FF ratio method may be that roots contribute with a significantly larger litter input to the forest floors at the poor site Ulborg than at the richer sites (paper II).

4.3.3 Phosphorus and forest floor characteristics

Some of the studies have pointed at P as an important soil property in relation to forest floor chemistry, C content, and turnover rate in Denmark (papers I, II, and III). Forest floor C/P ratios were related to mineral soil P concentrations, and P concentrations in beech and Norway spruce litter accordingly varied considerably between soils of different P status (paper III). Soil P was also among those soil fertility variables which best explained the variation in forest floor C content (paper I). In the litterbag study (paper III), C/P ratios in beech and Norway spruce litter exhibited a characteristic converging trend during decomposition towards C/P ratios of 400-500. Such a converging trend was also reported Rustad and Cronan (1988) and Prescott et al. (1993). Litter with initially low C/P ratios (200-400) had fairly constant ratios or decreased slightly in P relative to C, while litter with initially high C/P ratios (900-1000) increased considerably in P relative to C. In the most P-poor beech litter, P was not only retained relative to C, but was also imported from external sources. This pattern may indicate that P concentrations in fresh litter were insufficient for microorganisms at the most P-poor site, and P deficiency could be one of the reasons for slower decomposition at this site. Soil P concentrations were also among those soil properties which best explained the variation in forest floor C content.

Another feature was the C/P ratio patterns encountered in litter layers and fermentation/humus layers of forest floors in the thinning trials at three sites of different soil P status (paper II). It was hypothesized that the considerable mass of roots in forest floors at the most P-poor site through mycorrhizal associations might be able to access organic P. This would be an effective method for the trees to circumvent the litter - nutrient pool - plant cycle without involving free-living saprophytic organisms (Dighton 1991), and it would enable the trees to compete effectively for P. The question remains, however, what implications the competition between mycorrhizal fungi and free-living decomposers could have for cycling of other nutrients and for C storage. Gadgil and Gadgil (1971, 1975) and Parmelee et al. (1993)

suggested that nutrient and moisture competition between mycorrhizal roots and free-living decomposers could lead to suppression of free-living decomposers. The apparent P depletion of forest floors by mycorrhizal roots may have promoted accumulation of C and other nutrients in forest floors at this relatively P-poor site.

The bioassay for microbial availability of N and P (paper V) indicated that a much greater proportion of total P than of total N was potentially accessible to microorganisms in partially decomposed forest floor material. Whereas amino-N may react with polyphenols, thereby becoming unavailable for microorganisms (Kelley and Stevenson 1995), greater potential availability of total P could be due to less immobilization in such recalcitrant compounds. The microbial P availability tended to reflect the P status of soils, but P availability differences were much smaller than expected from soil P concentrations and forest floor C/P ratios. This calls for further studies of the relationship between a conventional forest floor quality variable as the C/P ratio and microbial activity.

5 Perspectives

The studies demonstrated that tree species and soil properties are important factors to consider when estimating C storage in forest floors, and the thinning intensity was also found to influence C storage to some extent. Forest floor characteristics are relevant in relation to nutrient cycling, pedological processes, regeneration success, and also in relation to their potential as sinks for increasing atmospheric CO_2 levels. Soil properties are permanently associated with a site and can only be modified to some extent, e.g. by fertilization, liming, and tillage, whereas different tree species may be selected by forest managers, and the thinning intensity may be altered by management as well.

5.1 Nutrient cycling

Stands with large forest floors may have a significant proportion of the nutrient pool stored in unavailable form for the vegetation (Büttner 1997). At nutrient-poor soils, forest floors immobilized the greatest amount of nutrients due to slow turnover (paper I, II, III, IV). However, in forests at nutrient-poor soils fast cycling of nutrients would be desirable in order to maintain a stable supply of plant available nutrients. A positive effect of tree species on remobilization of nutrients would therefore be of special interest at such sites, and this emphasizes the need for extensive soil gradients to study tree species effects. Some of the tree species included in this work exhibited consistent differences in element storage along an extensive gradient in soil nutrient status. These effects were attributed to inherent differences among tree species in litter quality which were maintained along the soil gradient. Litterfall C contents were smaller for deciduous than for coniferous species when derived from stem volume increment, but measured litterfall in five of the tree species at two sites suggested that tree species were more similar with respect to litterfall C contents (Table 1). Consequently, turnover rates for C and nutrients must be affected by tree species along the gradient in soil nutrient status. Both at fertile and less fertile soils, selection of different conifers for planting could result in different rates of nutrient cycling and in the end lead to varying nutrient immobilization in forest floors. For instance, selection of grand fir would lead to less

immobilization of nutrients in forest floors than selection of Norway spruce, Sitka spruce or lodgepole pine. There was some indication of interaction between effects of tree species and soil nutrient status. Lodgepole pine differed from the other species by accumulating equally large amounts of C irrespective of soil nutrient status, and oak had low and more constant forest floor C contents than other tree species along the soil gradient. Assuming that litterfall was comparable among tree species, turnover rates would be relatively slower in lodgepole pine with increasing soil nutrient status, whereas oak stands would have relatively faster turnover than other tree species with decreasing soil nutrient status. However, there was no evidence that the influence of tree species was generally smaller at nutrient-poor than at nutrient-rich soils. The results suggest that inherent tree species properties also makes it possible to manage for fast remobilization of nutrients at infertile soils, where extensive accumulation of organic matter may immobilize a relatively large amount of the nutrient pool.

5.2 Soil formation.

Several studies have found that mineral soil properties were affected by tree species as reviewed by Binkley (1995). For instance, differences in mineral soil C content may develop in the long-term under the influence of different tree species. This could be due to greater incorporation of forest floor C in some species, e.g. through burrowing activity of earthworms (Judas et al. 1997), but Son and Gower (1992) mainly attributed tree species differences in soil C concentration to differences in root litter production. The considerable variation among tree species in forest floor mass and chemistry (paper I) may also influence mineral soils (Nihlgård 1971, Binkley and Valentine 1991). Nørnberg et al. (1993) reported that sandy soils of the same origin were more acid under spruce than under oak due to differences between the species in forest floor chemistry and mass. Podzolization processes were more evident in the soil under spruce than under oak, which was attributed to greater leaching of phenolic compounds from spruce forest floors. Leached organic solutes from forest floors may also contribute to soil development by increasing the weathering rate of soil minerals (Lundström and Öhman 1990). Raulund-Rasmussen et al. (1997) reported that nutrient release due to weathering was positively related to the concentration of dissolved organic carbon (DOC) in natural solutes from forest floors, and DOC concentrations differed among tree species and soil types. Consequently, tree species might differ in their influence on weathering rates due to the variable forest floor chemistry. Based on the differences in pH and C contents of forest floors (paper I), tree species like lodgepole pine and Sitka spruce might be expected to have a greater acidifying effect on mineral soils in the long-term. Similarly, the impact of forest floors would be greatest at nutrient-poor soils with large stored amounts of acid organic matter. If base cation exchange and leaching is enhanced by the build-up of thick, acid forest floors, this may be detrimental for future productivity, whereas increased weathering rates may be considered positive provided the mobilized nutrients are not subsequently leached from the ecosystem. Increased weathering rates would probably be of greatest ecological significance at nutrient-poor sites, where the demand for increased nutrient availability is greatest. However, in poor soils dominated by quartzitic minerals, the weathering potential will be low in

absolute terms. In such acid soils poor in other minerals than quartz, extensive forest floor build-up might further increase the acidity and enhance the podzolizing processes, thus creating a feedback loop which may promote further accumulation of elements in forest floors with unfavourable pH and C/nutrient ratios.

5.3 Regeneration

The importance of forest floor characteristics for regeneration of forest stands was recognized early (e.g. Hesselman 1927). High steady state levels in forest floor mass may have been reached in mature forests, and forest floors are not as favourable a rooting medium for seedlings as the upper mineral soil horizon in moderately moist climates (Fleming and Mossa 1994). After drought periods it may also be observed that dry forest floors are rewetted slowly and heterogeneously which could prolong drought periods for seedlings. In addition, thick forest floors at nutrient-poor sites may be greatly infiltrated by roots (Staaf 1988, paper II), thus further exacerbating the poor moisture conditions for seedlings. In relation to use of natural regeneration or direct seeding without soil cultivation, it might therefore be better to manage for more moderate forest floor build-up, e.g. through the selection of tree species or through the thinning treatment. Strong thinning intensity decreased the C content and the root mass in forest floors at two of three sites (paper II), and nutrient release was probably greater in the strongly thinned stands due to higher rates of turnover. Forest floor turnover rate and nutrient release may increase even more following the drastic microclimatic changes imposed by clear-cutting. At the same time the vegetation cover is sparse, and nutrient leaching may occur (Krause and Ramlal 1987). It might be expected that the more continuous vegetation cover associated with shelterwood regeneration would result in a better proportion between nutrient release rates and the potential for nutrient uptake in the vegetation. Prescott (1997) found that N mineralization rates in alternative silvicultural treatments, e.g. shelterwood cutting, were more comparable to rates in old-growth forest than to rates in a clearcut. The maintenance of site nutrient capitals during regeneration calls for further studies, but the thinning intensity may provide a measure for management of forest floors. An effect of thinning would be most interesting for regeneration and planting at nutrient-poor sites, where forest floors are thick and are infiltrated by roots. At such sites, moderately increased nutrient release rates would be desirable. However, it was found in paper I that the effect of thinning treatments were weaker at the site with the greatest C accumulation in forest floors. At more nutrient-poor sites, the changes in microclimatic conditions or litter nutrient status imposed by thinning could be insufficient to affect nutrient cycling significantly.

5.4 Forest floors as sinks for CO_2

The C content in forest floors reflects the relationship between C added in litterfall and C lost by microbial decomposition. Consequently, forest floors may act as both sources and sinks for atmospheric CO_2. Anthropogenic emissions of CO_2 are predicted to lead to global warming, which could result in faster decomposition, thereby exacerbating the increase in atmospheric CO_2 (Luxmoore et al. 1993). However, higher temperatures might also increase the input of

litter C thus offsetting the influence of faster decomposition on forest floor C contents. Different scenarios for C storage in soils have been predicted according to the relative alteration of litter production rates and decomposition rates (Liski 1997). Carbon storage in forest floors varied considerably among tree species (paper I) implying that forest floors of some tree species are greater sinks for CO_2 than those of other species. Forest floors were estimated to contain approximately 20% of total soil C (forest floor C + mineral soil C) above ground water level in Finnish forests, and total soil C approximately equalled the C content in stand biomass (Liski and Westman 1995). Mineral soil and biomass C contents should be considered together with forest floor C contents to achieve an overall estimate of C storage in forests. However, as regards forest floors, tree species like lodgepole pine and the spruces had a greater potential for storage of C than oak, beech, and grand fir. Tree species which would be considered unfavourable with respect to nutrient cycling and regeneration success may instead be rated highly if forest management aims at increasing the C storage in forest floors. It appears possible to manipulate C storage in forest floors by selection of different tree species, but in light of the predicted rise in temperatures it is necessary to know more about how differences in C storage among tree species are affected by alterations in litter production rates and decomposition rates. Soil properties also influenced C storage in forest floors. Afforestation of nutrient-poor soils could lead to greater C storage in forest floors than afforestation of nutrient-rich soils where faster turnover would stabilize C contents at a lower level. Again, differences in mineral soil and biomass C contents between soils of different nutrient status should be included to achieve estimates for whole ecosystems.

The potential additional storage capacity of forest floors might contribute to reduce the increase in atmospheric CO_2 concentration, but other objectives in forest management may be in conflict with increased C storage. However, this issue may exemplify that interests concerning forest floor conditions may not always be identical, and that ratings like “good” or “bad” conditions apply to the specific objectives in forest management.

6 Future research

This thesis found indications that forest floor build-up and decomposition in seven tree species were affected to different extents by soil properties. This implies that tree species-specific models should probably be used to predict C storage or decomposition in forest floors along gradients in soil nutrient status. More research into tree species-soil interactions is needed to explore the factors which cause litter of some tree species to be of so low quality for decomposers that variation in nutrient concentrations is insufficient to result in faster decomposition.

Forest floors contain a part of the C stored in dead organic matter, but significant amounts may also be stored in the mineral soil. It is essential to increase the knowledge of C storage in mineral soils as affected by soil properties and silviculture if forests should be managed for binding of atmospheric CO_2. The possible interactions between forest floor and mineral soil C storage would also be a relevant subject. For instance, to what extent does forest floor characteristics influence C storage in the mineral soil?

Another pending aspect of forest floors is their potential use as ecosystem indicators. Readily observable forest floor features, e.g. thickness and morphology, are often used by foresters as a rough indicator of site nutrient regime. This thesis demonstrated a relationship between forest floor element contents and soil nutrient status, suggesting that forest floors may be usable as indicators of soil conditions. It remains, however, to identify relevant readily observable features and to validate their use as indicators in a scientific framework. This framework should consider the variation in forest floor characteristics imposed by different tree species and stand treatments.

Effects of tree species were studied in monoculture stands, and effects of mixing litter from different tree species were not directly addressed in the studies. However, litter mixing occurs in forest floors of mixed-species stands and in forest floors of monoculture stands with a vigorous ground flora. Some studies have indicated that greater diversity of substrates for decomposer organisms may result in a synergistic effect on decomposition, and more knowledge of these possible interactions is desirable, as litter mixing occurs in most forest ecosystems.

Studies of the influence of litter quality and the soil environment on occurrence and activity of the different groups of decomposer organisms are also necessary to explore the mechanisms behind variable forest floor element contents and turnover rates. Results in this thesis suggested that the activity of decomposers differed according to tree species, the soil-induced litter quality within a tree species, and the conditions determined by properties of mineral soils. This could be due to differences in species representation and in the number of individuals, but there may also be synergistic effects due to co-occurrence of some species. Respiration rate bioassays such as the one used in this work may be valuable tools for evaluation of the decomposer response to litter quality or environmental conditions. For instance, to examine if the conventional chemical indicators of litter and forest floor quality (e.g. C/N and C/P ratios) are relevant parameters for the activity of decomposer organisms.

Soil nutrient status, e.g. P status, was important for nutrient immobilization and cycling in forest floors. Fertilization and liming may provide means to improve the nutritional and environmental conditions for decomposer organisms, but experiments have not supported many generalizations about the influence of fertilization and liming on decomposition and nutrient cycling. This could in part be due to differences between short-term and long-term effects. It would be relevant to examine whether long-term effects of fertilization and liming are in fact attainable.

Forest floor nutrient accumulation was not similarly affected by the thinning intensity at all studied sites, possibly due to influence of other site-specific factors. The benefit in regeneration success from greater nutrient release and thinner forest floors in strongly thinned stands would probably be greatest at poor sites. The strong thinning intensity used in shelterwood cutting might increase turnover rates enough to improve conditions for regeneration without leading to extensive nutrient losses. Research is needed to explore the response of forest floors to stand treatments, in order to develop biogeochemically sustainable silvicultural systems. Especially, it should be studied whether it is also possible to increase the

turnover rate of forest floors by stronger thinning intensity on poor soils where nutritional and physical properties of forest floors may most hamper regeneration success.

7 Conclusions

The results supported the hypothesis that tree species influence forest floor chemistry, nutrient availability, and element content strongly. The differences in C contents must also reflect that turnover rates differed among tree species. Seven tree species exhibited consistent differences in forest floor chemistry and element contents along an extensive gradient in soil nutrient status suggesting that inherent differences in litter quality among tree species is an important factor. The microbial N and P availability in forest floors was also influenced by tree species.

The study of thinning intensity and forest floor C, N, and P contents was for the most part consistent with the hypothesis that C, N, and P contents decrease with increasing thinning intensity. However, at the most nutrient-poor of three sites, the effect of thinning intensity was small compared with the accumulated amounts of C, N, and P. The effect of thinning was most likely due to improved microclimatic conditions, as the slight changes in forest floor chemistry suggested that thinning influenced storage of C, N and P little through improved litter chemistry.

Forest floors were also affected by soil nutrient status. The chemistry variables were related to properties of mineral soils, suggesting that litter quality within tree species varied according to soil nutrient status. Element contents decreased and turnover rates increased with increasing soil nutrient status. However, this picture appeared to be less pronounced in some tree species indicating that other factors than nutrient status were limiting for turnover rates. A litterbag study for the most part supported the hypothesis that soil nutrient status may influence the rate of turnover both through litter chemistry and through the specific soil environment. Decomposition of beech litter was most consistent with this hypothesis while decomposition of Norway spruce litter was not influenced through the litter quality. Nutrient release during decomposition was mainly related to the litter chemistry which differed according to soil nutrient status. Different aspects of soil fertility were important for forest floor C content and turnover rate along soil gradients in Denmark and in coastal Washington, USA. In Denmark, soil properties such as mineral soil pH, concentrations of P and Ca, and texture were important, whereas turnover rate was closest related to soil N capital and soil C/N ratio in USA.

The studies suggested that it is possible to manage chemistry and element contents of forest floors by selection of tree species and by the thinning intensity. The influence of tree species may be consistent along extensive gradients in soil nutrient status although some interaction between tree species and soil nutrient status was indicated. Further studies are required in order to examine if the thinning intensity also influences forest floor build-up at nutrient-poor soils.

8 Acknowledgements

The studies in papers I and V were financially supported by The European Commission (grant no. 93.60.DK.004.0).

I want to thank my supervisor, Karsten Raulund Rasmussen, for his catching commitment and for encouraging and supporting guidance throughout this study. I have appreciated the constant backing in spite of changing surroundings.

Several persons have been a great help with field and lab work. My sincere thanks are due to Lena Troelsen for skilful work and constructive advice in the laboratory, and for good company during many days of litterbag cleaning. Camilla Hoppe also did a fine job in the laboratory with the respiration rate bioassay. The assistance of Peter Theis Hansen, Jens Holst-Nielsen, Mads Jensen, Mikkel Eriksen, and Egon Madsen with forest floor sampling, processing of samples for laboratory analyses, and preparation of litterbags is greatly acknowledged. Maj-Britt Johansson, Swedish University of Agricultural Sciences, gave me good advice about the litterbag technique and analyses of organic chemical fractions of litter.

Thanks are also due to The Danish Forest and Landscape Research Institute for allowing me to use the tree species trials and the thinning trials for the studies, and for providing stand data. Jørgen Bille-Hansen, Danish Forest and Landscape Research Institute, kindly allowed me to use some unpublished litterfall data.

Cindy Prescott deserves my special gratitude for an interesting and very worth-while stay at Department of Forest Sciences, University of British Columbia. Thanks for instructive experiences from working together and for valuable comments on some of my manuscripts .

This Ph.D. study was carried out at Unit of Forestry at Frederiksberg and Hørsholm. Thanks to people in both places for a pleasant and stimulating environment. Also thanks to the people at Department of Forest Ecology, Danish Forest and Landscape Research Institute, for letting me take part in things and for contributing to an enjoyable and interesting atmosphere. Special thanks are due to Morten Ingerslev, Henrik Vejre, and Ingeborg Callesen for constructive advice and comments and not least for the good company.

Lastly, great thanks to my family for putting up with me and for encouragement throughout the last years.

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Paper I

Forest floor chemistry and element contents as affected by seven tree species and a soil fertility gradient

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Canadian Journal of Forest Research (submitted)

FOREST FLOOR CHEMISTRY AND ELEMENT CONTENTS AS AFFECTED BY SEVEN TREE SPECIES AND A SOIL FERTILITY GRADIENT

Manuscript for Canadian Journal of Forest Research

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Abstract

Vesterdal, L., and Raulund-Rasmussen, K. 1997. Forest floor chemistry and element contents as affected by seven tree species and a soil fertility gradient. Can. J. For. Res. XX: XX-XX.

Forest floor chemistry and element contents were examined in stands of two deciduous species and five conifer species replicated at seven sites along a soil fertility gradient. There were consistent differences in chemistry and element contents among the tree species. Lodgepole pine (*Pinus contorta* Dougl.) forest floors had the least favourable chemistry and the greatest element contents, whereas oak (*Quercus robur* L.) forest floors had a more favourable chemistry and the lowest element contents of all species. Differences in chemistry and element contents between sites of low nutrient status and sites of intermediate to high nutrient status were also great. Forest floor pH and C/P, C/Ca, and C/K ratios were related to mineral soil pH and nutrient concentrations, respectively, and forest floor carbon content was negatively related to mineral soil fertility variables. Carbon content was closest related to texture, pH, and concentrations of P and Ca in the mineral soil. The C content of lodgepole pine and oak forest floors tended to be less affected by the soil fertility gradient. The results suggest that C storage and immobilization of nutrients in forest floors may be managed along an extensive soil gradient by selection of the proper tree species.

Key words: forest floors, chemistry, element contents, tree species, *Abies grandis*, *Fagus sylvatica*, *Picea abies*, *Picea sitchensis*, *Pinus contorta*, *Pseudotsuga menziesii*, *Quercus robur*, soil fertility gradient.

Introduction

The forest floor plays an important part in nutrient cycling, as nutrients are released during litter decomposition and rendered available to plants. Forest floor mass reflects the relationship between the rate of litter production and the rate of litter decomposition (Olson 1963), and the forest floor mass corresponds with the amount of nutrients immobilized in forms unavailable to plants. This may be harmful for forest regeneration and productivity in the long-term. Müller (1879) defined two morphological types of forest floors, mull and mor, which were associated with fertile soils and nutrient-poor soils, respectively. Later studies have also reported that forest floor mass and chemistry differ according to soil type within a single tree species (Ovington 1953, Florence and Lamb 1974, Staaf 1987). Forest floors at nutrient-poor soils have a greater mass and are more poor in nutrients relative to carbon compared with forest floors at nutrient-rich soils. This may be due to an effect of soil nutrient status on the quality of the litter (Lukumbuzya et al. 1994, Sanger et al. 1996), and an effect of soil properties on the decomposer community (Schaefer and Schauermann 1990). Forest floor mass and chemistry of different tree species on the same soil type may also differ significantly (Ovington 1954, France et al. 1989, Son and Gower 1992, Muys et al. 1992, Prescott and Preston 1994), probably due to inherent differences in litter quality among tree species (Kiilsgaard et al. 1988, Nordén 1994). Studies of tree species differences within single sites have led to a general belief that certain tree species tend to develop relatively thick, acid forest floors (mor), whereas others develop relatively thin and less acid forest floors (mull). It is possible, however, that such an effect of tree species on forest floors will not persist along more extensive soil gradients. Only few studies have explored the effects of tree species on forest floors along an extensive gradient in soil properties, as this requires even aged stands of different tree species replicated along a soil gradient, and many tree species are not growing naturally or cultivated along extensive soil gradients. A large-scale study by Muys and Lust (1992) indicated a strong effect of tree species on forest floor type, while the effect of soil texture was smaller. In contrast, Raulund-Rasmussen and Vejre (1995) reported that forest floor chemistry and nutrient contents of four tree species differed considerably between a sandy and a loamy soil, while the effect of tree species was weaker. The difference among tree species appeared to be smaller at the sandy site than at the loamy site.

In the present study we examined forest floors in stands of seven tree species replicated at seven sites along a gradient in soil nutrient status. The study focused on two aspects of forest floors: chemistry (pH and C/nutrient ratios) and element contents. The specific aims were to explore i) forest floor chemistry and element contents of different tree species along an extensive gradient in soil fertility, ii) relations between forest floor chemistry and mineral soil properties, and iii) relations between forest floor carbon content and soil fertility variables.

Materials and methods

Sites and tree species

Even aged monoculture stands of seven tree species replicated at seven sites were included in

the investigation. The tree species were beech (*Fagus sylvatica* L.), oak (*Quercus robur* L.), Norway spruce (*Picea abies* (L.) Karst.), Sitka spruce (*Picea sitchensis* (Bong.) Carr.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis* Lindl.), and lodgepole pine (*Pinus contorta* Dougl.). The seven sites distributed throughout Denmark were chosen in order to obtain gradients in soil properties. All sites are included in a tree species trial established by The Danish Forest and Landscape Research Institute in 1964/65 (Holmsgaard and Bang 1977). The eastern sites, Christianssæde (Chr) (Mollic Hapludalf), Holsteinborg (Hol) (Oxyaquic Hapludalf), and Frederiksborg (Fre) (Typic Argiudoll), are the most nutrient-rich with soils developed from loamy weichselian till (soil classification according to Soil Survey Staff (1992)). At Chr, the parent material was calcareous (28% $CaCO_3$ in the C horizon). Among the western sites, Løvenholm (Lov) and Tisted Nørskov (Tis) (both Typic Haplumbrepts) are intermediate with respect to nutrient status. These soils are developed from weichselian till with textures between loamy sand and sand. The sites Lindet (Lin) (Typic Quartzipsamment) and Ulborg (Ulb) (Typic Hapluhumod) are the most nutrient-poor with soils developed from a parent material of sandy till deposited during the Saale glaciation. Selected soil properties for the sites are given in Table 1. All seven trials are on almost level ground. Climatically, the sites are rather similar, although the annual precipitation varies slightly. Mean annual temperatures are 7.5-7.7°C for Lin, Ulb, Tis, Lov, and Fre and 8.4°C for Hol and Chr, and mean annual precipitation ranges from 610 mm to 890 mm (Hol≈Chr≈Lov<Tis<Fre≈Lin<Ulb). All data climate are from The Danish Meteorological Institute. The gradients in temperature and precipitation are not coinciding with the gradient in soil fertility, and effects of soil properties were consequently not regarded as confounded with effects of macroclimate. At four of the sites (Chr, Fre, Lov, Tis), the land use was agriculture prior to afforestation. At Hol and Lin, the sites were forested (beech forest and oak coppice, respectively), whereas the area at Ulb was former heathland. Before planting, all sites but Hol were cultivated by ploughing, and at these six sites forest floors are known to originate from the present stands. Understory shrubs were not present in the stands to any great extent, and except for a moss layer in some of the fir and spruce stands at the nutrient-poor sites, grasses and some herbs only covered the ground coherently in the oak stands (Lange 1993).

Forest floor sampling

During winter 1994/95, area-based sampling of the forest floors was carried out. Ten subsamples per stand were selected randomly and collected by using a frame covering 25 cm x 25 cm. Contamination with mineral material was avoided. The forest floor depth was registered by measuring each of the four sides in subsample pits and calculating a stand average. The subsamples were dried at 60°C, and herbaceous litter, cones/fruits, twigs and larger roots were excluded before weighing. The 10 subsamples per stand were pooled to one sample for chemical analysis.

Chemical analyses

Ground samples of forest floor material were analysed: pH by potentiometry in a 1:10

suspension of organic matter and 0.01M $CaCl_2$; total carbon and nitrogen by dry combustion (LECO CHN 1000 Analyzer); total phosphorus by flow injection analysis; total calcium, potassium and magnesium by flame atomic absorption spectroscopy (AAS). Phosphorus, Ca, K, and Mg were measured after digestion of samples with concentrated nitric acid in a microwave oven.

Soil samples from genetic horizons in one central soil pit at Hol, Lov and Tis were analysed: pH by potentiometry in a 1:2.5 suspension of soil and 0.01M $CaCl_2$; particle size distribution by a combined pipette and sieve method (clay, <2μ; silt, 2-20μ; fine sand, 20-200μ; coarse sand, 200-2000μ); total C by dry combustion and weighing of evolved carbon dioxide; total N by the Kjeldahl method; P by flow injection analysis after extraction with 0.1M sulfuric acid for two hours; exchangeable Ca, Mg, and K by AAS after extraction with 1M NH_4NO_3. Soil data for Chr are from Raulund-Rasmussen and Vejre (1995) and soil data for Ulb, Lin and Fre are from Raulund-Rasmussen (1993). Horizon-weighted nutrient concentrations were calculated for two soil depth strata (0-50 cm and 50-100 cm) in order to quantify the nutrient status. Mineral soil pH and texture (percent clay, silt, fine sand, and coarse sand) were represented by horizon-weighted values for the two soil depth strata.

Statistics

Effects of tree species and site on forest floor chemistry, volume weight, and element contents were tested by one-way ANOVA with site as block factor, as the experimental design lacked tree species replication within sites. Consequently, no degrees of freedom were left for testing interaction effects. Duncan's multiple range test was used to compare means. To test correlations between quantitative soil properties and forest floor chemistry, and also enable testing of interaction effects, forest floor pH and C/nutrient ratios were subsequently tested by use of the procedure GLM with tree species as class variable and mineral soil pH or nutrient concentrations as quantitative variables. Correlations between mineral soil properties and forest floor C contents were tested similarly. Tree species means were compared by use of Tukey's studentized range test. C/Ca ratios were logarithmically transformed prior to statistical analysis in order to normalize and homogenize variances. To test whether a site effect on forest floor volume weight was connected with variation in forest floor depth, volume weight was also analysed using GLM with tree species as class variable and depth as quantitative variable. A correlation matrix with the selected mineral soil properties was constructed using the procedure CORR (n=7). All analyses were carried out using SAS (SAS Institute 1993).

Results

Forest floor chemistry and volume weight

All forest floor chemistry variables and volume weight were affected by tree species ($p < 0.001$) (Table 2). Lodgepole pine forest floors generally had the highest C/nutrient ratios (*i.e.* C/N, C/P, C/Ca, C/K, C/Mg) and the lowest pH, while beech and oak forest floors had the

lowest C/nutrient ratios. In detail, forest floors of lodgepole pine and Sitka spruce had higher C/P ratios than forest floors of the other tree species, and the C/P ratio for lodgepole pine was also significantly higher than for Sitka spruce. Lodgepole pine also differed from all other species by having the significantly highest forest floor C/Ca ratios. Douglas-fir and Sitka spruce had fairly high C/Ca ratios as well, whereas beech, oak and grand fir had relatively low C/Ca ratios. C/Ca ratios in Norway spruce forest floors were intermediate. C/N ratios in lodgepole pine forest floors were significantly higher than in forest floors of all other tree species, but grand fir forest floors had high C/N ratios as well. C/K and C/Mg ratios varied rather similarly among the tree species. Lodgepole pine had higher C/K ratios than all other species and Sitka spruce had higher C/K ratios than Norway spruce, beech and oak. C/Mg ratios were significantly higher in lodgepole pine and Sitka spruce than in Norway spruce, grand fir, beech, and oak. Lodgepole pine forest floors also had higher C/Mg ratios than forest floors of Douglas-fir. Forest floor pH was significantly higher in beech than in all other tree species but grand fir, and lodgepole pine had the most acidic forest floors of all tree species. Between the two extremes, forest floor pH values in grand fir and Norway spruce were relatively high whereas Sitka spruce, Douglas-fir, and oak forest floors had lower pH values. Forest floor volume weights were lowest in the deciduous species and highest in the spruces, Douglas-fir, and grand fir. Lodgepole pine forest floors were intermediate, although volume weights were not significantly lower than in Douglas-fir and Sitka spruce.

Site affected pH and C/N, C/P, and C/Ca ratios strongly ($p < 0.001$), whereas the effect on C/Mg ratios, C/K ratios, and volume weight were weaker ($p < 0.05$) (Table 2). Ulb and Lin had high C/P and C/Ca ratios, whereas Lov and Tis had low C/P ratios, and Lov, Tis, and Chr had low C/Ca ratios. The site differences for C/N ratios were opposite, as Ulb and Lin had significantly lower C/N ratios than the other sites. C/K and C/Mg ratios did not exhibit the same patterns as the other C/nutrient ratios. C/K ratios were highest at Tis and lowest at Fre, and C/Mg ratios were highest at Lin and lowest at Ulb. Forest floor pH values were significantly lower at Ulb and Lin than at the other sites. The differences in volume weight were smaller among sites than among tree species. However, volume weights were higher at Lin than at Lov and Chr, and forest floors at Ulb had higher volume weight than forest floors at Chr. Although volume weights tended to be higher at the sites with deep forest floors, forest floor depth did not explain any variation in volume weights significantly.

Forest floor pH was positively related to soil pH (0-50 cm), and C/P, C/Ca, and C/K ratios in the forest floors were negatively related to concentrations of P, Ca, and K, respectively, in the soil (Table 3). The correlations were fairly similar for the two soil depth strata except for pH and C/P ratios, which were only significantly correlated with properties in the upper soil stratum. The negative correlation between forest floor C/N ratios and soil N was not quite significant, and C/Mg ratios were not significantly correlated with soil Mg. There were no significant interactions between tree species and soil properties, *i.e.* forest floors of the seven tree species were not affected differently by the gradient in soil nutrient status. However, there

were significant tree species differences in all forest floor chemistry variables along the gradient in soil nutrient status. The studied tree species explained a great part of the variation in forest floor C/nutrient ratios and pH, and tree species differences were almost similar irrespective of soil depth stratum. Tree species differences along the individual gradients were not quite as pronounced as in the ANOVA including sites and tree species (Table 2), but the same pattern was found (Table 3).

Forest floor element contents

The contents of C, N, P, Ca, Mg, and K in forest floors were strongly affected by tree species ($p < 0.001$ except $p < 0.01$ for Mg content) (Figs. 1-2). Sites also affected element contents strongly ($p < 0.001$ except $p < 0.01$ for Ca content). Forest floor C contents were higher for lodgepole pine than for all other tree species, and among the remaining species, Norway spruce and Sitka spruce had higher C contents than beech, grand fir, and oak. Oak had a lower amount of forest floor C than all other tree species but grand fir. Douglas-fir had intermediate C contents and did not differ significantly from either the spruces or beech. Among sites, Ulb and Lin had by far the largest forest floor C contents. The contents of N and P in the forest floors exhibited a pattern fairly similar to that of C. Lodgepole pine differed less from the other coniferous species in N, P, K, and Mg contents than in C content, and beech forest floors had relatively high contents of K and Mg. The pattern among tree species in forest floor Ca content was very different from the pattern in C content. Oak, grand fir, lodgepole pine, and Douglas-fir had low contents of Ca in the forest floors, whereas beech and Norway spruce forest floors had large contents of Ca.

Mineral soil properties explained a significant part of the variation in forest floor C content (Table 4). Logarithmic transformation of some soil properties gave the best fit for the linear models. Carbon contents decreased with increasing mineral soil pH and increasing concentrations of P, Ca, K, and Mg, but C contents were positively related to C and N concentrations in the soil. Forest floor C content was only related to K and Mg concentrations in the lower soil stratum. Carbon content was also correlated with soil texture, as the C content decreased with increasing percent clay, silt, and fine sand and increased with increasing percent coarse sand. The tree species had accumulated different amounts of C along the gradients in soil properties, and the effect of tree species was consistent for all soil properties and both soil depth strata. The effect of tree species interacted significantly with some of the soil properties, *i.e.* C accumulation was not affected to the same extent for all tree species by these soil properties (Table 4 and Fig. 3). The C contents of lodgepole pine forest floors were not significantly related to percent silt or C and P concentrations in the upper soil stratum, nor were the C contents related to percent silt or Ca, K, and Mg concentrations in the lower soil stratum. Carbon contents for Norway spruce, Sitka spruce, grand fir, Douglas-fir, and beech were all affected similarly and significantly by these soil properties, and C contents were more affected than for lodgepole pine ($p < 0.05$). The C content of oak forest floors was

intermediately affected by soil properties in case of significant interaction, and C content was only significantly correlated with soil P concentration (0-50 cm) and percent silt (50-100 cm). Tree species differences exhibited the same pattern as in the ANOVA (Fig. 1), also in case of significant interactions. The soil concentrations of P, Ca, K_{50-100}, Mg_{50-100}, C, and also pH_{0-50}, percent silt, and percent coarse sand were properties that explained a great part of the variation together with tree species. As expected, some of these soil properties were intercorrelated (Table 5). Within both soil strata, pH was correlated with P and exchangeable Ca, and K was correlated with Mg and percent clay. Soil pH was also correlated with textural properties in the upper soil stratum. Within the lower soil stratum, both K and Mg were very closely correlated with textural properties (clay, silt and coarse sand), and Ca and P were also intercorrelated. Soil C and N concentrations, and percent coarse sand tended to be negatively correlated with the other properties.

Discussion

Forest floor chemistry and volume weight

The tree species had different pH and C/nutrient concentrations in the forest floor irrespective of the gradient in mineral soil properties. This suggests that tree species possess a specific, genetically determined litter quality which contributes to differences in forest floor C/nutrient ratios and pH. The two deciduous species had low and similar C/nutrient ratios, and only forest floor pH was significantly higher for beech than for oak. A similar pH difference between beech and oak was also reported by Ovington (1953). The conifer species exhibited great variation in both C/nutrient ratios and pH. This is probably due to differences in litter nutrient concentrations among tree species as reported by Alban (1982) and Ovington (1953, 1954). Gloaguen and Touffet (1982) found that C/N ratios in both the litter and the forest floor of lodgepole pine were higher than C/N ratios in litter and forest floors of beech and Douglas-fir. These findings correspond with ours and emphasize the link between litter and forest floor chemistry. Our forest floor C/Ca ratios in grand fir, Douglas-fir, Sitka spruce, and lodgepole pine are also in accordance with Ca concentrations in foliage litter reported by Kiilsgaard et al. (1988). However, differences in forest floor nutrient status among tree species may not only reflect differences in litter nutrient status. The initial nutrient status of litter has probably been mediated to some extent by variable decomposition rates and nutrient dynamics (Ovington 1954, Rustad 1994). The presented forest floor chemistry variables suggest that forest floors of different tree species offer variable conditions for decomposing organisms, and that tree species may have implications for soil development due to differences in forest floor element contents and acidity (Binkley 1995).

The deciduous species had less compact forest floors than the conifers as indicated by the volume weights, and among the conifers, lodgepole pine with its larger needles had less compact forest floors than Norway spruce and grand fir. This is in contrast to results reported by Alban (1982), who found that volume weights of aspen (*Populus tremuloides* Michx.), red pine (*Pinus resinosa* Ait.), and jack pine (*Pinus banksiana* Lamb) forest floors did not differ

from volume weights of white spruce (*Picea glauca* (Moench) Voss) forest floors. Liski (1995) found a volume weight of Scots pine forest floors close to the figures obtained in this study for Norway spruce and grand fir. The stand investigated by Liski (1995) was much older than the stands in this study, and in tree species building up thick, mor-like forest floors, increasing volume weight with time is expectable. Differences among tree species in forest floor volume weight may reflect differences in decomposition rate, as mull-like forest floors should have a more loose structure than mor-like forest floors. However, forest floor volume weight appeared to be more connected with differences in foliage litter morphology.

Forest floor chemistry and volume weights also varied among sites (Table 2). Volume weights tended to be highest at the nutrient-poor sites, and forest floor morphology at these sites were correspondingly more mor-like. Forest floors with lower volume weights were found at the richer sites where the morphology was mull-like. The variation in forest floor chemistry among sites indicated that it might be due to variation in soil nutrient status, and some of the forest floor chemistry variables were significantly related to soil properties (Table 3). Ovington and Madgwick (1957) similarly found correlations between pH in the mineral soil and pH of both litter and forest floors. The correlation between forest floor pH and mineral soil pH tended to be weaker with increasing soil depth, and forest floor C/P and C/K ratios were also closest correlated with P and K concentrations in the 0-50 cm soil stratum. This soil stratum constituted the main rooting zone for Sitka spruce at Fre, Ulb, and Lin (Pedersen 1993), and it probably influenced litter nutrient status and subsequently forest floor nutrient status strongest. The significant correlations between mineral soil Ca, K, and P concentrations and forest floor C/Ca, C/K, and C/P ratios, repectively, may be attributed to a soil-induced effect on litter quality (Perala and Alban 1982, Boerner 1984). Remarkably, forest floor C/N ratios were lowest at the two sites most poor in other nutrients than N. This pattern may be partly due to differences in N deposition among sites, as Hovmand et al. (1994) found higher N deposition at Lin than at Ulb and Fre (30-40 kg ha^{-1} yr^{-1} compared with 20 kg ha^{-1} yr^{-1}). Forest floor C/N ratios were apparently not solely determined by soil N capital, but might also be influenced by local N emission sources. In an area with less N deposition, Prescott et al. (1997) even found an inverse relationship between mineral soil N capital and forest floor N concentrations in Douglas-fir forests. Since litterfall N concentrations were positively related to soil N capital, N dynamics during decomposition in their study and the present may have greater effect on forest floor C/N ratios than soil N and litterfall C/N ratio. C/Mg ratios also appeared to be more affected by other site factors than soil Mg, *e.g.* by deposition of marine salts. Pedersen (1993) reported that the annual flux of Mg in throughfall (kg ha^{-1} yr^{-1}) in Sitka spruce stands could be ranked Ulb (15.5)>Lin (12.7)>Fre (6.4). This may explain the low C/Mg ratios at Ulborg, but does not correspond with the high C/Mg ratios at Lin.

Forest floor element contents

Forest floors of the seven tree species had very variable element contents (Fig. 1), indicating that tree species may affect nutrient immobilization in forest floors considerably. Nitrogen and

P contents appeared to be closely related to the C content, whereas great variation in C/Ca, C/Mg, and C/K ratios among tree species resulted in different patterns among species in Ca, Mg, and K contents than in C contents (Figs. 1-2). Carey et al. (1982) correspondingly reported that N and P contents for *Pinus radiata* D. Don forest floors were mainly related to forest floor mass, whereas K and Mg contents were also a product of varying concentrations in the forest floors. Species differences in forest floor Ca content support results of Alban (1982) and Wilson and Grigal (1995) that Ca contents for spruce species and deciduous species were higher than for pine species despite diverging trends in forest floor mass. The differences in C contents correspond reasonably well with reports that pine and spruce species tend to have greater forest floor masses than Douglas-fir and grand fir (Ovington 1954, Gloaguen and Touffet 1980). However, Eriksson and Rosén (1994) found no significant differences in forest floor mass or nutrient contents between Norway spruce and grand fir. The higher C contents in beech stands than in oak stands support the observation made by Ovington (1954) that beech tends to build up larger forest floors than other deciduous species. Nihlgård (1971) reported that the C content of forest floors increased when beech stands were replaced by Norway spruce stands, and that this might contribute to an increase in podzolization processes due to increased production of organic acids. In this study, Norway spruce forest floors also had greater C contents and were more acid than beech forest floors. However, forest floor N, P, Ca, K, and Mg contents were not significantly lower for beech than for Norway spruce. The coniferous species exhibited a great range in forest floor C, N, P, and Ca contents, and results did not support the common conception that conifer stands store more elements in forest floors than deciduous species per se. The consistent tree species differences in forest floor C content along the soil gradient (Table 4) suggest that differences among these seven tree species may apply to soils of different nutrient status. This points to the conclusion that nutrient immobilization in forest floors may be managed by selection of the proper tree species. However, the significant interaction between tree species and certain soil fertility variables (*e.g.* P concentration, Fig. 3), implies that differences among other groups of tree species might be influenced by soil nutrient status. This emphasizes the necessity of conducting forest floor studies along soil gradients in order to support generalisations about the influence of tree species.

The differences among sites in forest floor element contents were marked (Figs. 1-2), and the sites fell into two groups: The two sites with the most nutrient-poor soils had larger element contents than the other sites. Staaf (1987) found that the forest floor mass in beech stands were nine to ten times greater at a nutrient-poor, sandy soil than at a nutrient-rich, clayey soil, and Vesterdal et al. (1995) found a six-fold difference in the C contents of Norway spruce forest floors which was attributed to differences in soil properties. Forest floor C contents decreased with increasing soil fertility as indicated by the negative correlations with pH, exchangeable bases and percent clay and silt (Table 4). Carey et al. (1982) explored the effects of site on forest floor organic matter in stands of *Pinus radiata*, but they only found a weak negative effect of exchangeable Ca in the mineral soil, possibly due to great variation in stand

and climate characteristics. In this study there was only little climatic variation among sites, and increasing soil fertility was associated with decreasing C accumulation in forest floors. The only exception was the positive correlation between C content and soil N concentration. The apparent positive effect of soil N on C accumulation was probably due to the fact that soil N concentrations were highest at the two sites which had the largest C contents and were least fertile in other respects. It may be concluded, however, that high soil N concentrations were not associated with low forest floor C contents. In contrast, Prescott et al. (1997) found an indication of decreasing C and N contents in Douglas-fir forest floors with increasing soil N capital. The lower C content at the more fertile sites might be a result of translocation of organic matter from the forest floor to the mineral soil, *e.g.* as a result of faunal activity. However, the positive correlation between mineral soil C concentration and forest floor C content indicated that low C contents at some sites were not solely explained by incorporation of C in the mineral soil. Some of the soil fertility variables in this study were highly intercorrelated, but soil texture, Ca and P concentrations, and pH (0-50 cm) appeared to be important fertility variables. These soil properties may have important nutritional and environmental effects on the diversity and activity of decomposer organisms which in turn affect C accumulation (Schaefer and Schauermann 1990, Raubuch and Beese 1995). The forest floor chemistry variables pH and C/P ratio were correlated with soil pH and soil P, respectively, suggesting that forest floor quality might also be more favourable for free-living decomposer organisms at nutrient-rich soils. Concentrations of K and Mg in the upper soil stratum were not related to forest floor C contents, and the correlations with K and Mg concentrations in the lower soil stratum might rather be due to strong intercorrelation with percent clay and silt (Table 5). It may be questioned to what extent soil properties in 50-100 cm depth are of ecological significance to forest floor C accumulation. Obviously, this soil stratum has a limited direct influence on forest floors if both roots and decomposer organisms are mainly present in the upper soil stratum. However, the lower soil stratum is more representative of the soil parent material than the upper stratum, and the correlations emphasize the indirect effect that parent material characteristics may have on forest floors. It must be stressed that although the correlations explained a significant part of the variation encountered in the forest floors, they were not able to explain the actual processes involved or to point out single soil variables as the main explanatory variables. However, the correlations do indicate that forest floor C contents for the most part were related to soil nutrient status.

Forest floors of lodgepole pine, and in some cases also forest floors of oak, tended to be less affected by some of the soil fertility variables (Fig. 3). The fairly constant forest floor C content in lodgepole pine stands suggests that soil-induced changes in litter quality, or differences in the decomposer communites along the soil gradient were unable to mediate the effect of inherent litter quality on C storage in this tree species. Oak forest floors had the lowest C contents along the gradient, and the lack of correlation with some of the soil fertility variables indicates that C contents tended to increase less with decreasing nutrient status than for beech, Douglas-fir, grand fir, and the spruces. The inherent properties influencing C

accumulation in these two tree species appear to be very strong. Thus, C accumulation in some tree species may be more weakly modified by a gradient in soil fertility than C accumulation in the other tree species.

Large differences in element contents were found although stands were only 30 years old. Different element contents were also reported for plantation stands of the same age by Son and Gower (1992), and Muys et al. (1992) found differences in forest floor mass between deciduous tree species already after 20 years. However, some forest floors may not be in steady state yet, *i.e.* that annual decomposition in the forest floor did not equal annual litter production. These forest floors would still be in an accretion phase. Olson (1963) suggested that the time necessary to achieve 95% of steady state is approximately 3/*k*, where *k*, the decomposition rate constant, is the ratio under steady state conditions of mean annual litter production and forest floor mass. Based on the forest floor C contents and litterfall C contents (J. Bille-Hansen pers. comm.) for beech at Fre and Ulb, values of *k* were 0.48 and 0.06, respectively. According to Olson's suggestion the time required to achieve 95% of steady state at Fre and Ulb would be approximately 6 years and 50 years, respectively. Steady state conditions may therefore not have been attained after 30 years for the tree species and sites with the most slow decomposition. Even greater differences among tree species and sites in forest floor C content may therefore be expected to develop in the future.

The observed tree species and site differences in forest floor element contents may be a result of both different litter production rates and different decomposition rates. Litter production was reported to be correlated with stem volume increment irrespective of tree species (Miller 1986). Other studies indicated that only conifers fitted this pattern as broadleaves had a fairly constant foliage mass and litterfall irrespective of volume increment (O'Neill and DeAngelis 1981; Pedersen and Bille-Hansen 1997), but a study of Sitka spruce stands did not confirm the relationship for conifers (Miller et al. 1996). Input of root litter to forest floors may also vary considerably. Vesterdal et al. (1995) found that Norway spruce stands on a relatively nutrient-poor soil had a much greater root mass in the forest floor than stands on more nutrient-rich soils. A larger input of root litter to forest floors at nutrient-poor sites may thus contribute to the great accumulation of forest floor C. Although it is difficult to generalize about litter production, different decomposition regimes must also be responsible for the varying forest floor C contents along the gradient in soil nutrient status. If litter production was in fact correlated with volume increment and was higher at the nutrient-rich sites than at the nutrient-poor sites, this could not account for the reported variation in C contents. Different decomposition rates must be mainly responsible for the C contents along the soil gradient. The more favourable chemistry of forest floors at nutrient-rich sites is in support of this interpretation. In contrast, differences in forest floor C contents between the less-productive deciduous tree species and the conifers may be a question of differences in both litter production and decomposition rate. Information on litter production is required in order to determine which factor is of greatest importance among the seven tree species.

Conclusions

Forest floors of the seven tree species exhibited consistent differences in chemistry and element contents along a gradient in soil nutrient status. This indicates that inherent tree species differences in litter quality influences forest floors at both nutrient-rich and nutrient-poor soils. Lodgepole pine forest floors had the most unfavourable chemistry and the greatest element contents, whereas oak forest floors had a more favourable chemistry and the lowest element contents of all species. Differences in forest floor chemistry and element contents between sites of low nutrient status and sites of intermediate to high nutrient status were also great. Forest floor pH and C/P, C/Ca, and C/K ratios were related to soil pH and nutrient concentrations, respectively, and forest floor C contents decreased with increasing soil nutrient status. Carbon contents were closest related to the soil properties texture, pH, and concentrations of P and Ca. While forest floor chemistry of the seven tree species were not differently related to soil properties, the C content tended to be less affected by soil fertility variables in lodgepole pine and oak. The results suggest that C storage and immobilization of nutrients in forest floors may be managed along an extensive soil gradient by selection of the proper tree species.

Acknowledgements

The study was financially supported by The European Commission, grant no. 93.60.DK.004.0. We would like to thank Lena B. Troelsen for carrying out most of the analyses, and Peter Theis Hansen, Mikkel Eriksen, Mads Jensen, and Egon Madsen for assistance with the field work. Thanks are also extended to Cindy Prescott for helpful comments on an earlier version of the manuscript.

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Table 1. Soil data for the seven sites.

	Depth (cm)	pH	Clay	Silt	Fsand	Csand	C	N	P	Ca^{2+}	Mg^{2+}	K^{+}
			(%)				(%)	($mg \cdot g^{-1}$)	($mg \cdot kg^{-1}$)	($cmol_{+} \cdot kg^{-1}$)		
Christianssæde*												
A1	0-5	3.8	12	10	49.1	28.9	2.8	2.1	110	4.6	0.6	0.12
A2	5-25	5.2	12	11	50.2	26.8	1.5	1.7	110	9.3	0.4	0.10
Bt	25-50	6.2	15	18	43.6	23.4	0.4	0.5	240	12.2	0.6	0.18
Btg	50-73	7.5	18	20	38.5	23.5			380	21.7	0.5	0.12
Ckg	73-110	7.7	9	16	52.6	22.4					0.3	0.07
Frederiksborg†												
Bt1	30-50	5.3	22.6	21.7	51.9	3.8	0.16	0.33	112	4.23	0.51	0.18
Bt2	50-85	5.4	24.0	29.0	44.4	2.6	0.06	0.24	182	4.02	0.72	0.18
Bt3	85-120	5.5	21.8	28.2	47.5	2.6	0.02		230	4.04	2.01	0.19
C	120-	5.1	25.2	25.1	46.3	3.3	0.02		263	3.72	2.87	0.20
Holsteinborg												
A	0-20	3.7	11.0	11.0	54.3	23.7	0.96	0.96	61	1.34	0.27	0.08
AE	20-55	4.5	9.5	10.0	53.1	27.4	0.55	0.71	84	5.21	0.69	0.09
E	55-85	5.4	10.5	6.0	74.1	9.4	0.04	0.22	99	4.67	0.57	0.10
Bt	85-120	6.1	28.0	21.0	39.5	11.5	0.14	0.37	181	15.53	0.97	0.19
C	120-	6.3	18.0	15.0	48.7	18.3	0.02		221	9.80	0.71	0.16
Lindet†												
A	0-6	2.9	2.5	5.8	45.0	46.8	4.97	2.70	10	0.26	0.37	0.15
E	6-18	3.9	3.9	6.2	46.3	43.6	0.79	0.34	6	0.02	0.02	0.01
Bhs1	18-22	3.7	9.4	7.4	40.2	43.0	1.24	0.55	9	0.04	0.04	0.03
Bhs2	22-60	4.2	6.5	6.5	47.1	40.0	0.96	0.47	37	0.02	0.02	0.03
Bs	60-80	4.4	4.8	2.5	48.7	44.0	0.14		38	0.01	0.01	0.02
C	80-95	4.5	1.3	1.3	53.5	43.9	0.04		25	b.d.*	b.d.	0.02
2C	95-	4.4	3.0	1.2	12.7	83.1	0.04		36	0.01	0.01	0.03
Løvenholm												
A	0-27	4.1	3.5	12.0	36.8	47.7	0.94	0.70	119	0.47	0.06	0.06
Bw	27-55	4.8	2.5	6.5	49.0	42.0	0.40	0.32	161	0.48	0.05	0.04
BC	55-70	4.7	4.0	9.0	48.7	38.3	0.08	0.23	223	0.21	0.03	0.04
Cg	70-	4.5	3.5	10.5	43.6	42.4	0.06		123	0.78	0.07	0.07
Tisted Nørskov												
Ap1	0-5	3.5	5.0	9.0	54.2	31.8	3.77	1.95	110	1.67	0.24	0.12
Ap2	5-21	4.1	2.5	8.5	57.7	31.3	1.68	1.00	76	0.82	0.07	0.03
Bw1	21-51	4.3	4.0	13.0	45.9	37.1	0.59	0.47	66	0.23	0.02	0.03
Bw2	51-88	4.2	5.4	12.3	41.4	41.0	0.10	0.11	31	0.38	0.03	0.06
C	88-	4.4	1.0	0.5	47.8	50.7	0.09		35	0.08	0.01	0.04
Ulborg†												
A	0-18	2.7	2.1	3.0	27.8	67.1	10.74	3.30	22	0.39	0.67	0.23
E	18-30	3.4	0.5	2.2	8.8	88.6	0.36	0.13	6	0.03	0.01	b.d.
Bh	30-34	3.5	10.9	3.8	17.1	68.2	6.98	2.40	24	0.20	0.13	0.09
Bhs	34-40	4.1	6.2	3.6	16.3	73.9	3.62	1.30	20	0.06	0.04	0.04
Bs	40-60	4.4	2.9	3.0	28.2	65.9	0.12	0.10	16	0.02	b.d.	0.01
BC	60-100	4.5	1.3	2.1	31.8	64.8	0.03		10	0.01	b.d.	b.d.
C	100-	4.6	0.9	2.5	23.6	72.9	0.01		11	0.01	b.d.	b.d.

Note: *Raulund-Rasmussen and Vejre (1995), †Raulund-Rasmussen (1993).
b.d.: below detection limit. Fsand: fine sand. Csand: coarse sand.

Table 2. Average values for C/N, C/P, N/P, and C/Ca ratios, pH, and volume weight (vw) in the forest floors of seven tree species and seven sites.

Species and sites	C/N	C/P	C/Ca	C/K	C/Mg	pH_{CaCl_2}	vw ($kg \cdot m^{-3}$)
Lodgepole pine	35.2*a*	674*a*	264*a*	805*a*	753*a*	3.48*d*	79*b*
Sitka spruce	28.7*bc*	530*b*	94*bc*	533*b*	648*ab*	3.99*c*	86*ab*
Norway spruce	26.4*c*	462*c*	77*cd*	412*cde*	480*cd*	4.26*bc*	109*a*
Douglas-fir	25.6*c*	452*c*	114*b*	462*bc*	546*bc*	3.98*c*	94*ab*
Grand fir	31.4*b*	434*c*	58*de*	438*bcd*	482*cd*	4.46*ab*	109*a*
Beech	26.8*c*	465*c*	48*e*	337*de*	396*d*	4.63*a*	55*b*
Oak	27.5*c*	440*c*	55*de*	315*e*	398*d*	3.97*c*	36*c*
Ulborg	24.8*b*	523*b*	137*ab*	453*bc*	419*c*	3.62*b*	88*ab*
Lindet	24.0*b*	586*a*	161*a*	506*ab*	620*a*	3.60*b*	105*a*
Holsteinborg	29.9*a*	485*bc*	106*bc*	453*bc*	525*abc*	4.17*a*	84*abc*
Tisted Nørskov	31.2*a*	453*c*	106*bc*	566*a*	574*ab*	4.23*a*	80*abc*
Christianssæde	30.5*a*	498*bc*	51*d*	437*bc*	549*ab*	4.27*a*	61*c*
Løvenholm	30.1*a*	434*c*	65*cd*	492*abc*	542*abc*	4.41*a*	71*bc*
Frederiksborg	30.8*a*	478*bc*	86*cd*	394*c*	473*bc*	4.47*a*	79*abc*

Note: Tree species means or site means in a column with the same letter are not significantly different ($p > 0.05$) based on ANOVA and Duncan's multiple range test.

Table 3. Test results for linear models explaining forest floor chemistry by variation in mineral soil properties (depth strata 0-50 cm and 50-100 cm) and by tree species. Tree species differences are shown according to a decrease in the respective forest floor chemistry variables.

Forest floor	Soil	Linear model: Forest floor chemistry = tree species$_i$ + b(soil property)				
chemistry variable	property			Hypothesis (1) b=0	Hypothesis (2) LP=SS=...=O	
		r^2	%r^2_{soil}	p	p	Tree species differences
pH	pH_{0-50}	0.59	32	<0.001 (+)	<0.001	*a* (B), *ab* (GF,NS), *abc* (SS), *bc* (DF,O), *b* (LP)
	pH_{50-100}	0.45	11	0.057	<0.001	*a* (B,GF,NS), *ab* (SS,DF,O), *b* (LP)
C/N	N_{0-50}	0.45	12	0.053	<0.001	*a* (LP), *ab* (GF,SS), *b* (O,B,NS,DF)
C/P	P_{0-50}	0.65	11	0.007 (-)	<0.001	*a* (LP), *b* (SS,B,NS,DF,O,GF)
	P_{50-100}	0.59	2	0.266	<0.001	*a* (LP), *b* (SS,B,NS,DF,O,GF)
log (C/Ca)	Ca_{0-50}	0.66	17	<0.001 (-)	<0.001	*a* (LP), *b* (DF), *bc* (SS,NS,GF,O), *c* (B)
	Ca_{50-100}	0.64	14	0.003 (-)	<0.001	*a* (LP), *b* (DF), *bc* (SS,NS,GF,O), *c* (B)
C/K	K_{0-50}	0.80	8	<0.001 (-)	<0.001	*a* (LP), *b* (SS), *bc* (DF), *bcd* (GF,NS), *cd* (B), *d* (O)
	K_{50-100}	0.76	4	0.027 (-)	<0.001	*a* (LP), *b* (SS), *bc* (DF,GF,NS), *c* (B,O)
C/Mg	Mg_{0-50}	0.57	4	0.169	<0.001	*a* (LP), *ab* (SS), *bc* (DF,GF,NS), *c* (O,B)
	Mg_{50-100}	0.57	2	0.259	<0.001	*a* (LP), *ab* (SS), *bc* (DF,GF,NS), *c* (O,B)

Note: r^2 = coefficient of determination, %r^2_{soil} = percent of model variation attributed to the soil property, b = slope, p = probability value. Tree species: LP, lodgepole pine; SS, Sitka spruce; NS, Norway spruce; DF, Douglas-fir; B, beech; GF, grand fir; O, oak. Tree species in brackets following the same letter are not significantly different ($p > 0.05$) based on Tukey's studentized range test.

Table 4. Significant linear models explaining forest floor carbon content by variation in mineral soil properties (0-50 cm and 50-100 cm, respectively) and by tree species. Soil properties that did not interact significantly with tree species (*i.e.* hypothesis 2 was rejected) were subsequently tested without the interaction term.

Linear model: C content = tree species$_i$ + b_i(soil property)

Soil property	Depth(cm)	r^2	Hypothesis (1) b=0 p	Hypothesis (2) $b_{LP}=b_{SS}=...=b_O$ p	Hypothesis (3) LP=SS=...=O p
pH	0-50	0.68	<0.001 (-)		<0.001
	50-100	0.52	0.016 (-)		<0.001
N conc.	0-50	0.58	<0.001 (+)		<0.001
log (C conc)	0-50	0.82	<0.001 (+)	0.025	<0.001
log (P conc.)	0-50	0.91	<0.001 (-)	<0.001	0.003
	50-100	0.72	<0.001 (-)		<0.001
log Ca conc.	0-50	0.67	<0.001 (-)		<0.001
	50-100	0.82	0.026 (-)	0.034	<0.001
log (K conc.)	0-50	0.47	0.151		<0.001
	50-100	0.85	<0.001 (-)	0.006	<0.001
log (Mg conc.)	0-50	0.45	0.422		<0.001
	50-100	0.82	<0.001 (-)	0.020	<0.001
% clay	0-50	0.55	0.004 (-)		<0.001
	50-100	0.59	<0.001 (-)		<0.001
log (% silt)	0-50	0.85	<0.001 (-)	0.033	0.012
	50-100	0.89	<0.001 (-)	0.002	0.002
% fine sand	0-50	0.64	<0.001 (-)		<0.001
	50-100	0.55	0.004 (-)		<0.001
% coarse sand	0-50	0.68	<0.001 (+)		<0.001
	50-100	0.67	<0.001 (+)		<0.001

Note: r^2 = coefficient of determination, b = slope, p = probability value, i=LP, SS, ..., O. Tree species abbreviations as in Table 3.

Table 5. Correlation matrices with Pearson correlation coefficients (n=7) for mineral soil nutrient concentrations, pH and texture in the depth strata 0-50 cm and 50-100 cm.

	C	N	P	Ca	K	Mg	pH	Clay	Silt	Fine sand
0-50 cm										
N	**0.87***									
P	-0.62	-0.31								
Ca	-0.31	0.18	0.72							
K	-0.03	0.30	0.48	0.69						
Mg	-0.10	0.33	0.38	**0.79***	**0.78***					
pH	-0.63	-0.26	**0.91****	**0.84***	0.65	0.51				
Clay	-0.46	-0.13	0.52	0.68	**0.86***	0.72	**0.76***			
Silt	-0.66	-0.42	0.66	0.49	0.67	0.41	**0.80***	**0.87***		
Fine sand	**-0.93****	**-0.76***	0.43	0.32	0.02	0.19	0.54	0.49	0.63	
Coarse sand	**0.84***	0.58	-0.59	-0.52	-0.48	-0.44	**-0.76***	**-0.83***	**-0.91****	**-0.88****
50-100 cm										
Ca			**0.89****							
K			0.55	0.39						
Mg			0.46	0.35	**0.96*****					
pH			**0.93****	**0.98*****	0.47	0.45				
Clay			0.57	0.48	**0.97*****	**0.99*****	0.57			
Silt			0.67	0.44	**0.92***	**0.86***	0.55	**0.89****		
Fine sand			0.29	0.34	0.58	0.50	0.31	0.52	0.27	
Coarse sand			-0.61	-0.50	**-0.98*****	**-0.93****	-0.56	**-0.96*****	**-0.86***	-0.71

Note: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

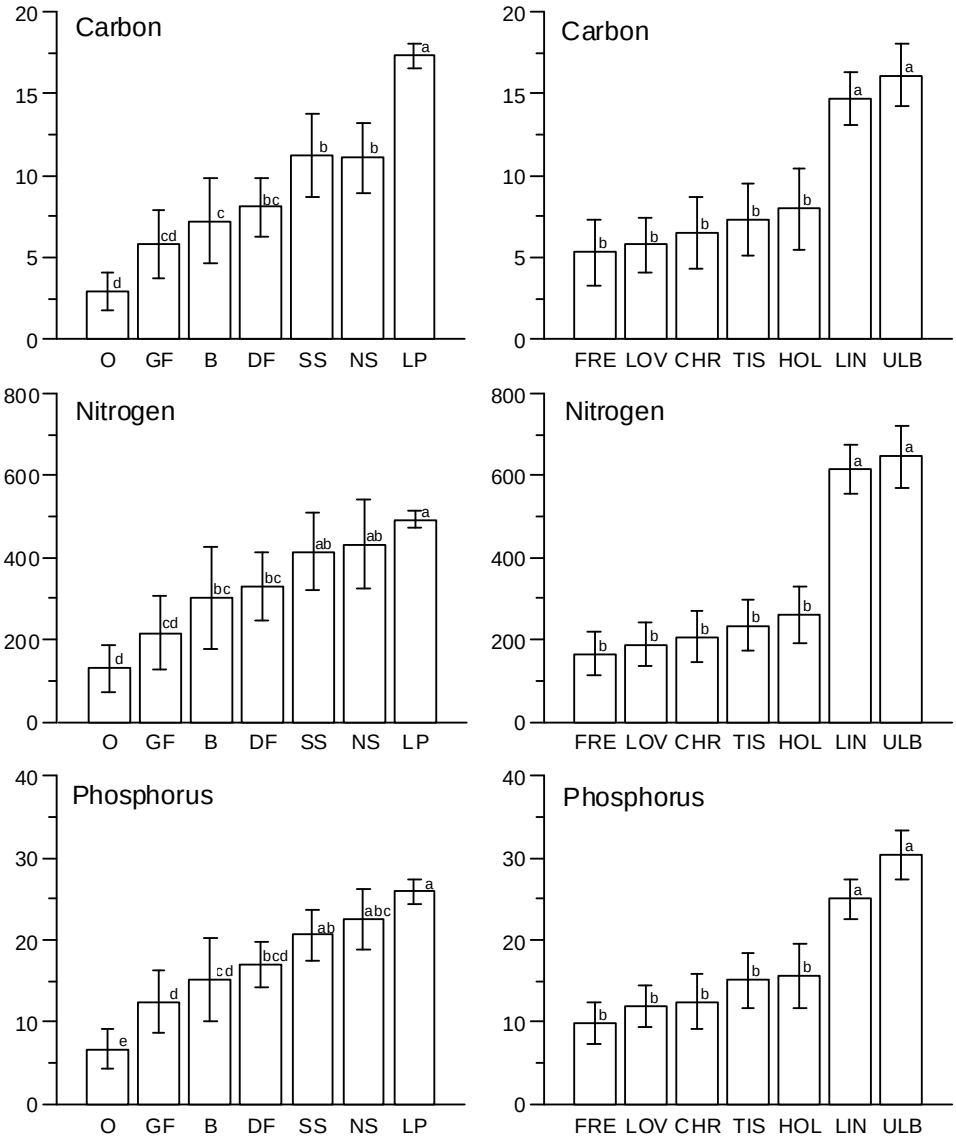

Fig. 1. The average C, N, and P contents in forest floors of seven tree species and seven sites (C in Mg·ha^{-1}, N and P in kg·ha^{-1}). Bars with the same letter are not significantly different (p > 0.05) based on ANOVA and Duncan's multiple range test. Error bars are one standard error of the mean. Tree species abbreviations: O, oak; GF, grand fir; B, beech; DF, Douglas-fir; SS, Sitka spruce; NS, Norway spruce; LP, lodgepole pine. For site abbreviations see text.

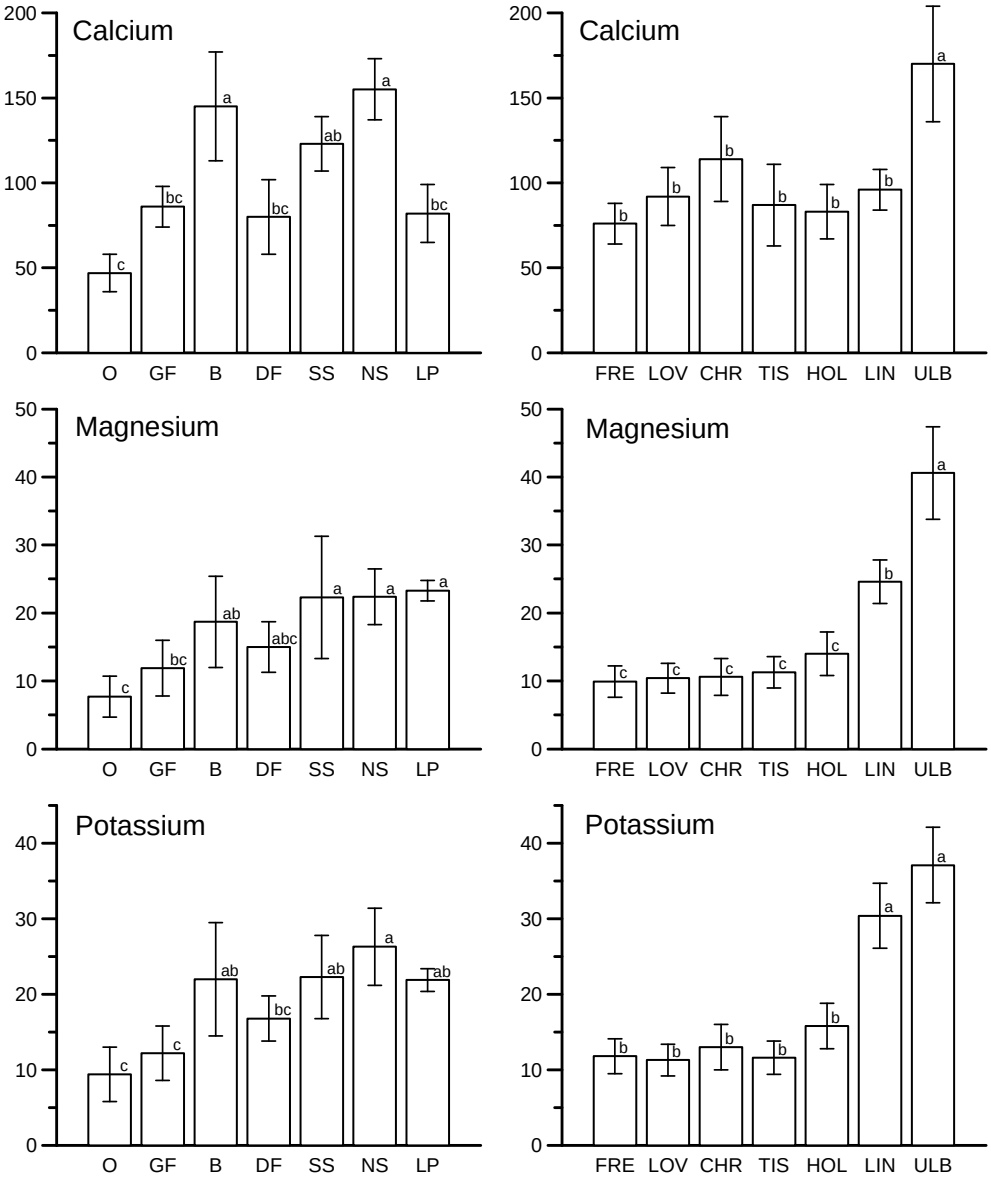

Fig. 2. The average Ca, Mg, and K contents in forest floors of seven tree species and seven sites (in kg·ha^{-1}). Bars with the same letter are not significantly different ($p > 0.05$) based on ANOVA and Duncan's multiple range test. Error bars are one standard error of the mean. Tree species abbreviations as in Fig. 1. For site abbreviations see text.

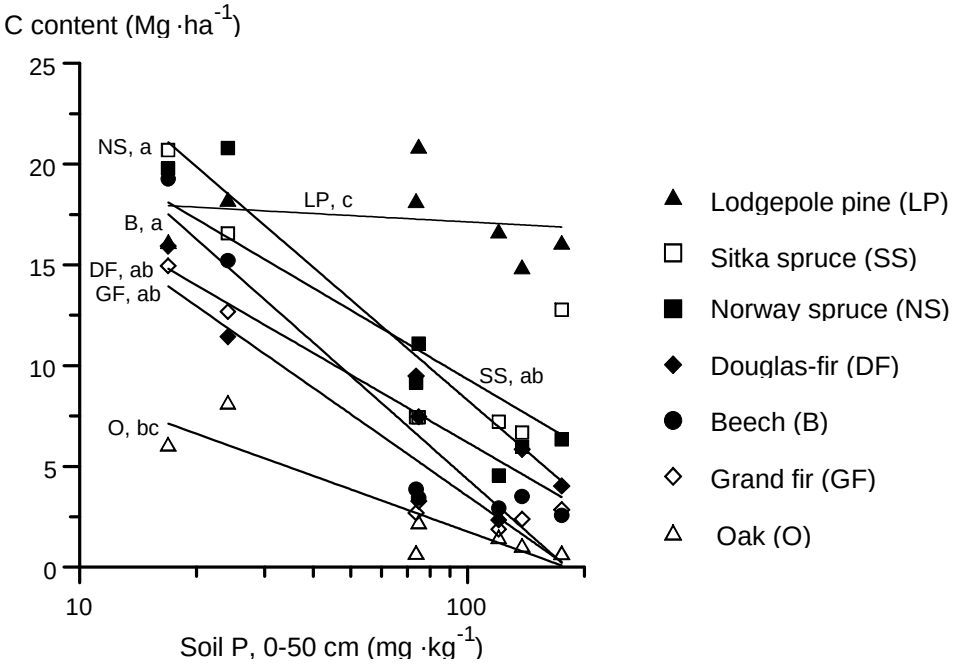

Fig. 3. Linear relations between soil P concentration (0-50 cm) and forest floor carbon content for the seven tree species. Lines with the same lowercase letter do not have significantly different slopes ($p > 0.05$) based on a general linear model and Student's *t* test.

Appendix 1. Forest floor depth, element contents, and pH for the 49 stands. See Table 3 for tree species abbreviations.

Site	Species	Depth (cm)	C ($Mg \cdot ha^{-1}$)	N	P	Ca	K	Mg	pH
				($kg \cdot ha^{-1}$)					
CHR	G	0.6	2.85	72	6.5	60	7.1	5.3	4.88
CHR	B	3.2	2.57	93	5.4	108	7.1	6.2	5.02
CHR	LP	3.8	16.11	431	23.8	169	24.1	22.7	3.58
CHR	DF	2.1	4.02	155	8.6	68	11.3	8.7	4.00
CHR	O	2.4	0.72	26	1.6	27	2.5	1.8	4.13
CHR	NS	1.9	6.33	49	15.5	162	19.4	14.9	4.42
CHR	SS	3.5	12.76	422	22.4	206	19.3	14.3	3.87
FRE	G	0.6	1.88	48	4.2	60	4.9	4.1	5.00
FRE	B	3.0	2.92	101	6.3	101	9.9	9.4	5.05
FRE	LP	3.9	16.67	434	22.2	47	20.3	21.0	3.46
FRE	DF	0.8	2.34	85	7.5	56	8.7	5.5	4.39
FRE	O	1.9	1.51	55	3.2	45	5.9	4.9	4.27
FRE	NS	1.0	4.54	166	12.0	107	18.5	13.7	5.02
FRE	SS	1.7	7.21	263	13.9	117	14.9	10.5	4.10
HOL	G	0.7	3.26	102	7.6	88	9.8	8.4	4.62
HOL	B	1.3	3.43	135	7.1	50	9.8	6.4	4.62
HOL	LP	4.3	20.88	595	34.4	66	27.2	28.8	3.51
HOL	DF	2.4	7.46	288	18.7	53	17.6	14.5	3.89
HOL	O	1.1	2.25	72	5.0	48	5.8	6.1	4.20
HOL	NS	2.6	11.09	394	22.6	156	23.8	22.1	4.27
HOL	SS	2.2	7.44	238	14.0	121	16.7	11.6	4.08
LIN	G	3.2	12.68	585	23.8	118	22.9	25.6	3.46
LIN	B	4.1	15.20	672	25.2	148	47.1	37.6	3.73
LIN	LP	5.7	18.25	517	25.0	90	24.6	25.8	3.36
LIN	DF	1.9	11.43	540	19.8	55	22.9	15.4	3.54
LIN	O	2.3	8.19	401	15.9	61	21.0	13.2	4.04
LIN	NS	4.1	20.79	887	35.3	102	46.1	31.2	3.34
LIN	SS	3.4	16.56	716	30.0	99	28.4	23.5	3.71
LOV	G	0.8	2.38	72	6.5	76	4.6	4.1	4.92
LOV	B	1.9	3.50	131	11.4	166	17.9	12.1	5.28
LOV	LP	4.0	14.90	446	22.7	103	17.4	17.9	3.57
LOV	DF	1.9	5.85	214	15.2	61	10.7	9.3	4.41
LOV	O	1.5	1.08	37	2.4	26	3.7	2.5	3.36
LOV	NS	1.4	5.97	230	14.4	124	12.7	17.1	4.85
LOV	SS	2.2	6.68	194	14.7	88	11.8	9.7	4.50
TIS	G	0.6	2.69	100	8.3	60	7.6	6.6	4.75
TIS	B	2.5	3.86	115	8.4	128	8.1	8.8	4.89
TIS	LP	4.8	18.19	504	26.8	60	16.9	20.0	3.51
TIS	DF	2.5	9.48	342	21.0	52	15.2	15.8	3.93
TIS	O	1.1	0.73	20	1.8	17	2.1	1.9	3.98
TIS	NS	2.3	9.14	11	22.8	213	18.8	14.7	4.38

Appendix 1(continued).

Site	Species	Depth	C	N	P	Ca	K	Mg	pH
		(cm)	($Mg \cdot ha^{-1}$)			($kg \cdot ha^{-1}$)			
TIS	SS	2.9	7.43	257	16.3	81	12.4	11.4	4.15
ULB	G	4.2	14.95	540	30.9	142	28.4	29.4	3.61
ULB	B	7.9	19.26	866	41.6	316	53.8	50.2	3.82
ULB	LP	6.5	16.16	533	26.4	37	23.1	27.3	3.36
ULB	DF	4.3	15.92	685	28.0	214	31.2	35.6	3.70
ULB	O	3.5	6.10	301	16.9	107	25.1	23.3	3.79
ULB	NS	5.2	19.78	797	35.8	222	45.0	42.9	3.53
ULB	SS	4.7	20.69	818	33.3	152	52.9	75.4	3.52

Paper II

Effects of thinning and soil properties on accumulation of carbon, nitrogen and phosphorus in the forest floor of Norway spruce stands

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Forest Ecology and Management 77: 1-10 (1995)

Paper III

Influence of soil type on mass loss and nutrient release from decomposing foliage litter of beech and Norway spruce

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Canadian Journal of Forest Research (submitted)

INFLUENCE OF SOIL TYPE ON MASS LOSS AND NUTRIENT RELEASE FROM DECOMPOSING FOLIAGE LITTER OF BEECH AND NORWAY SPRUCE

Manuscript for Canadian Journal of Forest Research.

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Abstract

Vesterdal, L. 1997. Influence of soil type on mass loss and nutrient release from decomposing foliage litter of beech and Norway spruce. Can. J. For. Res. XX: XX-XX.

Mass loss and nutrient release from decomposing foliage litter of beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst.) were studied at three sites along a soil fertility gradient. The influence of soil type through the litter quality and through the soil environment was separated by reciprocal transplantation of litter among soil types using the litterbag technique. Decomposition of beech litter was influenced by soil type through both litter quality and soil environment. Mass loss in beech litter was positively influenced by soil nutrient status. Decomposition of Norway spruce litter was not affected through soil type-induced litter quality, and the positive influence of a nutrient-rich soil environment was weak. Nutrient release in both tree species was greatly affected by soil type through the litter quality, as nutrient release was positively related to initial nutrient concentrations. Nutrient release was less affected through the soil environment, as it only influenced release of some nutrients, and the differences were not consistently related to soil nutrient status or mass loss. The influence of soil type on decomposition differed among the two tree species, suggesting that it may be more significant in species that produce relatively high quality litter.

Key words: decomposition, mass loss, nutrient release, litterbags, *Fagus sylvatica*, *Picea abies*, soil type, soil environment, litter quality.

Introduction

Decomposition of litter is an important process for the remobilization and cycling of nutrients in forest ecosystems. The decomposition process is influenced by factors related to macro- and microclimate, litter quality and activity of decomposing organisms which together determine the rate of decomposition and nutrient remobilization in forests. Differences in soil properties were long ago noted as being important for the morphology of forest floors. Müller (1879) described the occurrence of mull and mor forest floors at nutrient-rich and nutrient-poor soils, respectively, and attributed these features primarily to differences in the soil fauna communities. Handley (1954) also studied forest floor morphology in relation to soils, but did not conclude anything definitive about the rate of decomposition in mull and mor forest floors. However, later studies have suggested that soil properties may affect the mass of forest floors (Florence and Lamb 1974, Raulund-Rasmussen and Vejre 1995, Vesterdal et al. 1995) and the decomposition rate (Howard and Howard 1980, Boerner 1984a, Staaf 1987, Muys and Lust 1992). Soil properties may affect forest floor decomposition through 1) influencing the litter quality, *i.e.* the nutrient concentration (Boerner 1984b, Lukumbuzya et al. 1994, Nordén 1994) and the concentration of recalcitrant organic compounds like lignin and tannins (Flanagan and Van Cleve 1983, Sanger et al. 1996), and through 2) the microenvironment in which litter decomposition takes place including the communities of soil fauna and microorganisms taking part in the decomposition process. Soil fertility influences the species composition and biomass of microflora and microfauna (Schaefer and Schauermann 1990, Raubuch and Beese 1995), and the microbial activity may also be higher at nutrient-rich sites than at more nutrient-poor sites (Rastin 1994).

The extent to which soil properties influence litter decomposition has not been studied thoroughly. It is difficult to separate effects of soil properties in field studies, and in many studies, the influence of soil environment was confounded with effect of soil type-induced litter quality, effect of different tree species or effect of different climate. This study was designed to separate the effects of soil properties on litter decomposition and nutrient release into 1) influence of soil type-induced litter quality (origin of the litter) and 2) influence of the soil environment (litter incubation site) within a similar macroclimatic regime. This was done by reciprocal transplantation of foliage litter collected at three soil types using the litterbag technique (Berg and Ekbohm 1991, Johansson 1994). It was hypothesized that litter originating from a nutrient-rich site would decompose and release nutrients faster than litter originating from a nutrient-poor site, and that litter incubated at a nutrient-rich site also would decompose and release nutrients faster than litter incubated at a nutrient-poor site.

Materials and methods

Sites

The decomposition study was carried out in even aged, adjacent stands of beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst.) at three sites in Denmark with different soil nutrient status (Table 1). The Christianssæde site was the most nutrient-rich with

a soil (Mollic Hapludalf (Soil Survey Staff 1992)) developed from loamy and calcareous weichselian till, whereas the Ulborg site was the most nutrient-poor with a soil (Typic Haplohumod) developed from sandy till deposited during the Saale glaciation. The third site, Løvenholm, was considered of intermediate nutrient status with a soil (Typic Haplumbrept) developed from loamy sandy to sandy weichselian till. Forest floors were mor-like at Ulborg and mull-like at Christianssæde and Løvenholm, and data on forest floor nutrient accumulation at the three sites may be found in Vesterdal and Raulund-Rasmusssen (1997). Herb layers were absent in all six stands, but mosses were present in the Norway spruce stands at Løvenholm and Ulborg. The mean annual temperatures are 8.4°C at Christianssæde, 7.6°C at Løvenholm, and 7.5°C at Ulborg. The mean annual precipitation during the experimental period was 476 mm at Christianssæde, 498 mm at Løvenholm and 715 mm at Ulborg. The experimental period was much drier than indicated by the thirty-year mean annual precipitation (Christianssæde: 614 mm, Løvenholm: 614 mm, Ulborg: 890 mm) (all temperature and precipitation data from The Danish Meteorological Institute). The stands (approximately 0.25 ha each) are part of a tree species experiment planted 1964/65 (Holmsgaard and Bang 1977). Stand densities may were not identical at the three sites, but the effect of thinning is expected to be negligible compared with the effects of litter quality and soil type (Vesterdal et al. 1995).

Litter bag experiments

Foliage litter was collected in October 1994 from each of the six stands. Beech leaf litter was collected during litterfall by placing a tarpaulin on the ground and shaking branches and trees. Norway spruce neeedle litter was sampled from tarpaulins placed on the ground for three weeks. Green needles unmarked by senescence prior to abscission were sorted out. Two g dw (60°C for 48 hours) of foliage litter was enclosed in polyester litterbags measuring 13 x 15 cm and with a mesh size of approximately 1 mm. For each tree species, there were three types of litter according to the site of origin, and all three litter types of the two species were incubated at each site. The three beech and Norway spruce litter types were only incubated in stands of the respective tree species, *i.e.* litter of one species was not incubated in stands of the other species. In early December 1994, litterbags were placed on the litter layer in a randomized block design with ten 1 x 1 m blocks randomly distributed in each stand. Each block contained five sets of the three litter types for sampling at five different dates (total 900 litterbags: 2 tree species x 3 incubation sites x 3 litter origins x 5 sampling dates x 10 blocks). Litterbags were fastened to the forest floor by 10 cm long pins of high carbon steel and were collected twice a year in June and December for a period of 2.5 years. Litterbags were brought directly to the laboratory, and moss and mineral soil were removed. The contents were dried at 60°C for 48 hours and weighed, and the ten block replicates were subsequently pooled to one sample and ground before chemical analysis.

Chemical analyses

Total P, Ca, Mg, K and Mn concentrations in fresh and decomposing litter were analysed

following digestion with concentrated nitric acid in microwawe oven. Phosphorus in the diluted solution was measured by flow injection analysis, and the remaining nutrients were determined by atomic absorption spectroscopy. Total C and N were measured by dry combustion in a Leco CHN 1000 Analyzer. The water- and ethanol-extractable substances in fresh litter were extracted prior to determination of Klason lignin (Johansson et al. 1986) by treating the samples in a sonicator bath. Lignin concentrations were subsequently determined by hydrolysis (12 M H_2SO_4 at room temperature for 2 h and refluxed for 6 h after dilution to 0.358 M) and weighing of the residual solid material. All analyses were carried out in duplicate or triplicate.

Nutrient release from litter was calculated as

[1] $N = N_{in} - [(100\text{-}M)\ N_{dl}]$

where N represents the amount of a nutrient released during decomposition ($mg \cdot g^{-1}$ incubated litter), N_{in} is the initial nutrient concentration ($mg \cdot g^{-1}$), M is the mass loss (%), and N_{dl} is the nutrient concentration in decomposed litter (Entry et al. 1991).

Statistics

Mass loss within each tree species was analysed with a three way treatment structure to determine significance of main effects (litter origin, incubation site and sampling date) and interaction effects. Blocks were nested within incubation site and considered to be a random effect whereas other effects were considered to be fixed. Mass loss data (%) were log transformed in order to normalize and homogenize variances. In case of significant main effects, comparisons between means were performed by Student's *t* test. All analyses were carried out with the procedure MIXED in SAS (SAS Institute 1993). Differences between tree species were tested within incubation site and litter origin with the procedure TTEST. Effects of incubation site and litter origin on net nutrient release were initially tested by one-way analysis of variance in the procedure GLM with incubation site as block factor. Subsequently, the variation in nutrient release was tested in GLM with incubation site as class variable and the initial nutrient concentration as quantitative variable in order to explore whether variation in initial nutrient concentrations explained the differences in nutrient release.

Results

Litter quality

The litter quality of both beech and Norway spruce differed among the three sites of origin (Table 2). Beech foliage litter from Christianssæde and Løvenholm was generally more nutrient-rich than beech litter from Ulborg. The only exception was Mg which was found in highest concentration in the Ulborg litter. Beech litter from Løvenholm was considerably richer in the nutrients P, K, and Mn than the litter from Christianssæde. The amounts of water- and ethanol-extractable substances differed only little among the sites, but the lignin concentration was lowest in the Løvenholm litter. The litter quality differences were not quite as large in the Norway spruce litter, and it was more nutrient-poor than beech litter except for

Mn. Spruce litter from Ulborg was lower in P, Ca and Mn, but higher in N and Mg than litter from the other sites and the concentration of K was also higher in litter from Ulborg than in litter from Christianssæde. Like the beech litter, spruce litter from Løvenholm was higher in P, K, and Mn than litter from Christianssæde. The amounts of extractable organic substances and lignin were fairly similar for all three litter origins.

Mass loss

Mass loss in beech litter was significantly affected by both incubation site and litter origin, and there was no interaction effect of these two factors (Table 3). Sampling date was also highly significant, *i.e.* the mass decreased with time. There was a relatively large, significant interaction between time and incubation site compared with the main effect of incubation site. The interaction between time and litter origin was relatively small compared with the main effect of litter origin. Apart from an effect of sampling date, mass loss in Norway spruce litter was only weakly affected by incubation site. Mass loss through the incubation period is shown for both tree species by litter origin and incubation site in Fig. 1. As indicated by the interactions with sampling date for beech litter, the effect of litter origin was relatively consistent through the period, whereas the effect of incubation site increased through the period and was less consistent. Mass loss was consistently greater in beech litter collected at Løvenholm than in litter collected at Christianssæde, and except for the last sampling date, beech litter collected at Christianssæde decomposed faster than litter from Ulborg. Regarding incubation sites, beech litter decomposed faster at Løvenholm than at Ulborg during the last year of incubation. At Christianssæde, mass loss was either comparable to mass loss at Ulborg or comparable to mass loss at Løvenholm during the last year. However, at the end of the experiment mass loss at Christianssæde was as advanced as at Løvenholm while decomposition at Ulborg tended to be slowing down. Fig. 1b clearly shows that Norway spruce mass loss was completely unaffected by litter origin through the period. The effect of incubation site was only significant during the first half of the period. Norway spruce litter incubated at Christianssæde decomposed fastest, but it was not consistent whether decomposition was slower at Løvenholm or at Ulborg, or equally slower at both sites.

Mass loss in the two tree species exhibited different patterns when comparisons were made by the same litter origin or by the same incubation site (Fig. 2). Litter collected at Løvenholm and at Ulborg showed the most consistent tree species differences in mass loss, whereas beech and Norway spruce litter collected at Christianssæde decomposed at a very similar rate. Beech litter from Løvenholm had a greater mass loss than Norway spruce litter from the same site, whereas the opposite result was found for litter collected at Ulborg. Tree species comparisons for litter incubated at the same site showed a similar picture. At Christianssæde the species difference was inconsistent, but at Løvenholm beech litter had greater mass loss than Norway spruce since the end of the first year. At Ulborg, Norway spruce litter had greater mass loss than beech after 2 years and also at the first sampling date.

Nutrient release

Net release of nutrients from beech and Norway spruce litter was mainly influenced by the litter origin. This effect was due to differences in the initial nutrient concentrations as shown by the significant linear correlations in Figs. 3 and 4. For beech litter, net release of N, Mg, and Mn was also affected by incubation site (Fig. 3). Less N and Mg were released at Ulborg than at the other two sites, whereas Mn release was greatest at Christianssæde. Release of Mg, Mn, and Ca from spruce litter was also affected by incubation site (Fig. 4). Manganese release was greatest at Ulborg, and Mg release was greater at Christianssæde than at Ulborg. Calcium release for spruce litter interacted slightly with incubation site as release was less affected by initial Ca concentration at Løvenholm ($p < 0.01$). Calcium release at Christianssæde was greater than at Ulborg, but Ca release at Ulborg was still greater than at Løvenholm.

There was net immobilization of N and P in beech litter from Ulborg, and net Mn immobilization was found for both beech and spruce litter when the litter was initially low in Mn. C/P ratios for both beech and spruce litter tended to converge toward 400-500 regardless of origin or incubation site (Figs. 5a-b). C/N ratios were characterized by a general decrease regardless of litter origin and incubation site (Figs. 5c-d).

Discussion

Litter origin and litter quality

Litter quality of beech and spruce was clearly affected by origin of the litter (Table 2). Initial concentrations of P, Ca, K, and Mn in the litter appeared to be affected by soil nutrient status (Table 1) as also reported by Boerner (1984b), Nicolai (1988), and Nordén (1994). The litter from Ulborg had lower concentrations of P, Ca, and K (in beech only) than litter from the other two sites. The effect of soil Mg status on litter Mg concentration was probably mediated by higher deposition of Mg at Ulborg than at the other sites due to the proximity of the North Sea. The different Mn concentrations in litter at Løvenholm and Christianssæde may reflect higher Mn availability to plants in acid soils as at Løvenholm (Tyler 1976). Higher P concentrations in litter from Løvenholm than from Christianssæde despite comparable amounts of soil P may also be a result of different soil pH. Soil P might be stronger bound at Christianssæde (higher pH) and may consequently be less available to plants (Nihlgård and Lindgren 1977). Lignin concentrations were lowest in the beech litter from Løvenholm and highest in the beech litter from Ulborg. Sanger et al. (1996) reported a similar effect of soil fertility on lignin concentrations in Scots pine (*Pinus sylvestris* L.) needle litter, but differences in lignin concentrations were more pronounced in their study. The Norway spruce litters had very similar lignin concentrations despite the differences in soil fertility, but the sites could still be ranked according to lignin concentrations similar to beech litter.

Effect of litter origin on mass loss and nutrient release

The mass loss pattern for beech litter reflected the litter quality differences, whereas Norway

spruce mass loss was not affected by the differences in litter quality (Figs. 1a-b). These results suggest that soil properties were more likely to influence decomposition of beech litter than Norway spruce litter through the litter quality. The initial levels of N, P, K, and Mn in the beech litters appeared to be important for mass losses through the period. Berg (1986), Melillo et al. (1989), and Taylor et al. (1989) reported that the first phases of decomposition were mainly controlled by nutrient levels or readily available carbohydrates, whereas later stages were controlled by lignin decomposition. The effect of beech litter origin on decomposition during 2.5 years might therefore be attributed to differences in nutrient levels. In a 1-year decomposition study, Boerner (1984a) found initial N and P concentrations to be more important for mass loss in mixed-species litter than lignin concentrations. Along a soil gradient, Staaf (1987) also demonstrated a relationship between acid-base properties of beech leaf litter (pH and concentrations of Ca and Mg) and mass loss. Lignin concentrations may have been partly responsible for differences in mass loss toward the end of the experimental period (Berg et al. 1982, Rutigliano et al. 1996). Lignin concentrations also corresponded with the observed differences in mass loss, as a high initial lignin concentration will retard decomposition (Melillo et al. 1982). Norway spruce mass loss was remarkably unaffected by the variation in litter quality. One explanation could be that other litter properties in control of the initial stages of decomposition, *e.g.* solid carbohydrates and cellulose, did not differ among the three litter origins. Another explanation could be that an even greater variation in litter quality would be required to affect mass loss for Norway spruce litter. Lukumbuzya et al. (1994) also unexpectedly found that sugar maple leaf litter of different origin and with large differences in nutrient concentrations had the same mass loss. This led them to raise questions about the magnitude of quality difference required to result in mass loss differences within the same species, and whether litters of the same species always decompose at similar rates in the same environment. Mass loss results in this study suggest that the required magnitude of quality difference might differ between tree species, and the results for beech indicate that quality differences may affect decomposition rates regardless of the environment (the incubation site).

Nutrient release during decomposition may be expressed as a function of both mass loss and change in the concentration in the residual litter. Nutrient release from beech and Norway spruce litter was strongly affected by litter origin, *i.e.* the initial nutrient concentrations (Figs. 3 and 4). This occurred in spite of different mass loss patterns according to litter origin for the two species. Berg and Cortina (1995) also reported that N and P release from Scots pine litter was correlated with the initial concentrations of these nutrients although decomposition patterns were different. This suggests that there may be differences in the rate of nutrient cycling between sites of varying soil nutrient status despite almost similar decomposition rates. The significant correlations between nutrient release and initial nutrient concentration for Norway spruce indicated that nutrient release to a great extent occurs due to leaching or decomposition of labile substances during the studied decomposition stages. Prescott et al.

(1993) suggested that differences among litter types in N and P concentration mainly reflect different concentrations in the labile fraction, and this might also apply to the Norway spruce litter. Nutrient release and mass loss differences for beech litter were closer related. Beech litter from Løvenholm lost more mass and also released more N, P, K, and Mn than litter from Ulborg due to higher initial concentrations of these nutrients in the Løvenholm litter. Calcium release from beech litter was not as closely correlated with initial concentration as release of other nutrients (Fig. 3). The amounts of Ca released from beech litter collected at Løvenholm and Christianssæde were fairly similar despite a lower initial concentration in litter from Løvenholm. This probably reflects the nature of Ca as a structural component of litter (Blair 1988a), its release therefore being more controlled by mass loss than by initial loss of labile substances (Gosz et al. 1973). There were large differences in initial P concentrations for beech litter, and the P content increased slightly on an absolute basis in the P-poor beech litter from Ulborg (Fig. 3). This immobilization of P must be due to selective import from the surroundings as also observed by Staaf and Berg (1982). The differences in P release among litter origins resulted in a characteristic converging trend in C/P ratios for both beech and Norway spruce during decomposition (Figs. 5a-b). According to the initial P concentration, P was either immobilized or released relative to C resulting in more similar C/P ratios for all three litter origins after 2.5 years. Such a pattern for P was also reported from studies with different species (Blair 1988b, Rustad and Cronan 1988, Prescott et al. 1993). Gosz (1973) suggested a critical C/P ratio for decomposer organisms between 360 and 480 which might be close to the convergence value in this study, but Adams and Angradi (1996) and Blair (1988b) found indications of a lower critical C/P ratio. C/N ratios decreased for all litter orgins suggesting that differences in N concentrations were similarly limiting in litter from all sites. Both initial C/N and C/P ratios are important for decomposition rates (Enriquez et al. 1993), but the microbial demand for additional P to decompose beech litter from Ulborg may partly explain why litter from this site also had the smallest mass loss.

Effect of incubation site on mass loss and nutrient release

Mass loss was affected by incubation site in both tree species, but the effect was less consistent through the incubation period for Norway spruce litter than for beech litter (Figs. 1c-d). As climatic differences were small, these results indicate that decomposition was affected through the environment defined by the soil properties. For beech litter, the mass loss patterns among incubation sites were similar to the mass loss patterns among litter origins after the first year. As expected, mass loss was lowest at the most nutrient-poor site Ulborg, but mass loss was highest at Løvenholm and only intermediate at the site most rich in exchangeable base cations, Christianssæde. Only few litterbag studies have related mass loss within stands of the same species and the same climate to nutrient status of soils. Staaf (1987) found that mass loss in beech leaf litter was related to nutrient status of soils and attributed this to different conditions for microbial and microfaunal turnover. In contrast, Anderson (1973) found no difference in mass loss for beech litter incubated at a sandy and a clayey soil. The effect of incubation site for Norway spruce was not sufficient to overcome the increased

variation among litterbag replicates at the end of the incubation period, but mass loss still tended to be greater at Christianssæde than at Ulborg. The results suggest a weaker effect of incubation site nutrient status on the mass loss in Norway spruce litter. The incubation sites in this study represents communities of soil fauna and microorganisms which may colonize the litter. Decomposer biomass and species diversity were reported to be highest in nutrient-rich soil environments (Witkamp and van der Drift 1961, Schaefer and Schauermann 1990), and a low species diversity may result in slow decomposition (Setälä et al. 1988). Microbial biomass was also found to be positively correlated with the amount of exchangeable bases and pH (Raubuch and Beese 1995). These effects of soil properties on decomposition may be a reason for the slower decomposition at Ulborg. Based on soil properties, Christianssæde was expected to have the highest mass loss of the three sites, and incubation site differences for Norway spruce to some extent supported the hypothesis that mass loss would be greatest at the most nutrient-rich site. However, beech incubated at Løvenholm decomposed faster than at Christianssæde. One reason for this could be methodological, as the litterbag mesh size did not enable earthworm access. Exclusion of earthworms may have retarded decomposition more in beech than in Norway spruce. The forest floors and subsoils in beech stands were reported to have a greater earthworm biomass than in Norway spruce stands, but the earthworm biomass may be similarly low in beech and spruce stands on sandy, nutrient-poor soils as at Ulborg (Nordström and Rundgren 1973). Earthworm activity appeared to be much higher in the beech stand at Christianssæde than in the beech stand at Løvenholm, and a large amount of the unconfined leaf litter is probably incorporated in the soil at the former site. However, if earthworms were able to remove leaf litter from the litterbags, mass loss would rather represent litter disappearance from the forest floor than decomposition (Anderson 1973). Exclusion of earthworms from the decomposition process may nevertheless have decreased mass loss relatively at Christianssæde compared to natural conditions. Another reason for the fast beech litter mass loss at Løvenholm might be a positive effect of the nutrient-rich native litter on microbial activity in the incubated litter.

Incubation site affected release of N, Mg, and Mn from beech litter and release of Ca, Mg, and Mn from Norway spruce litter. The differences in nutrient release were not just a product of mass loss, and nutrient release was not clearly related to nutrient status of the sites. Magnesium concentrations in litter were high at Ulborg, and the lower release of Mg at this site probably reflects a greater throughfall flux of Mg due to the proximity of the North Sea (Pedersen 1993). The released fraction of the initial Mg content may not be lower, but due to a higher input of Mg, concentrations are maintained at a higher level at Ulborg. Manganese release was significantly highest at Christianssæde for beech and significantly highest at Ulborg for Norway spruce. These two sites both appeared to have lower Mn availability than Løvenholm, where Mn release generally was lowest. These release differences could be due to a greater selective demand among soil microorganisms at the sites with low Mn availability. Berg et al. (1996) reported that the initial Mn concentration in litter was related to long-term decomposition rates, possibly because Mn is important for the activity of lignin-degrading

enzymes in white-rot fungi (Perez and Jeffries 1992). Calcium release for Norway spruce was lowest at Løvenholm, and also increased less with increasing initial Ca concentration than at the other two sites. These relatively small differences may reflect the differences in mass loss after 2.5 years (Fig. 1d), as Ca release has been reported to track patterns of mass loss (Gosz et al. 1973). However, no such pattern was apparent for beech despite the mass loss differences among incubation sites. Nitrogen release from litter was generally low, and N release for beech was significantly lower at Ulborg than at the other sites due to net immobilization through the period. A higher microbial demand for N at Ulborg might result in a prolonged period of net N immobilization, and beech forest floors also had a lower C/N ratio at Ulborg than at Christianssæde and Løvenholm (Vesterdal and Raulund-Rasmussen 1997). Differences among sites in N deposition could also be involved, but then the same pattern would be expected for both tree species as seen for Mg release. Prescott et al. (1993) found no influence of N and P availability at incubation sites on N and P release. This agrees with the results for P release from this study. Although P concentrations in litter indicate great differences in P availability among sites, the released amounts of P were similar at all sites. The changes in C/N and C/P ratios over time also suggest that incubation site did not influence N and P dynamics as much as the initial N and P status of the litter. However, C/P ratios for beech and especially for Norway spruce tended to converge slower for the P-poor Ulborg litter when it was incubated at its site of origin. This also points at low P availability as a possible reason for slower mass loss at Ulborg.

Effects of soil type: Litter origin versus incubation site

The experiment with decomposition of beech leaf litter supported the hypothesis that soil type influenced decomposition both through litter origin and incubation site, while decomposition of Norway spruce needle litter only supported the hypothesis as regards effect of incubation site. The soil type therefore may influence early-stage decomposition of beech litter due to an effect on litter quality and due to an effect on the specific environment where decomposition takes place (Figs. 1a-d). These results agree with a similar study in beech stands along a soil gradient (Staaf 1987). However, Howard and Howard (1980) only found a small effect of incubation site and an even weaker effect of litter origin on birch (*Betula pendula* Roth) and oak (*Quercus robur* L.) decomposition when they compared a mull and a mor site. For birch litter originating from two sites (limestone and peat) and incubated at three different sites (limestone with mull, slate with moder, peat), Bocock and Gilbert (1957) reported influence of incubation site, but no effect of litter origin. A reason for these varying results may be that the soil gradients were not comparable. Interaction between litter origin and incubation site was not found in this study, *i.e.* mass loss was equally affected by origin at all incubation sites and was similarly affected by incubation sites for all litter origins. Contrary to this, Nicolai (1988) reported that beech litter decomposition in 1-cm mesh bags was more affected by limestone/sandstone origin when it was incubated at the limestone site. The lack of interaction in the present study may be due to the exclusion of macrofauna species at the nutrient-rich sites. It must be emphasized that results are relative estimates of decomposition under

standardized conditions, *i.e.* under influence of the same size fraction of decomposer communities.

The effects of litter origin and incubation site were not equally pronounced for beech and Norway spruce, suggesting that the influence of soil type may differ among tree species (Fig. 2). Beech thus decomposed faster than Norway spruce when the litter was collected or incubated at Løvenholm, whereas Norway spruce decomposed fastest when litter was collected or incubated at Ulborg. Interactions between tree species and soil type have also been reported from other studies. Bocock et al. (1960) found an effect of incubation site on mass loss in ash (*Fraxinus excelsior* L.) but found no effect in oak, and Bocock and Gilbert (1957) found an effect in lime (*Tilia cordata* Mill.) and birch while they found no effect in oak. These results all indicate that decomposition is controlled by whatever factor is most critical for decomposer organisms. If the litter is of low quality due to its tree species origin (*e.g.* Norway spruce), decomposition is less affected by soil fertility than in more favourable litter types (*e.g.* beech). Analogous to temperature and moisture interactions, the soil-induced nutrient status of litter or the soil microenvironment may be of little significance if specific tree species related litter properties set the quality low for decomposer organisms.

Nutrient release was most affected by soil type through litter origin, *i.e.* initial nutrients in the litter were more intimately involved in nutrient release than nutrients in forest floor or soil. This is not surprising, given the variation in initial nutrient concentrations among litter origins. The specific litter quality produced by Norway spruce and beech on a soil type was thus more likely to affect release of nutrients in the forest floor than the soil environment. However, it must be emphasized that this study only dealt with early stages of litter decomposition. It is possible that the influence of soil-induced litter quality on nutrient release decreases during later stages of decomposition, whereas the importance of the soil environment may increase (McClaugherty et al. 1985). A greater effect of soil type on Norway spruce mass loss might have been found if the study had included the later stages of decomposition. Much greater forest floor carbon contents in beech and Norway spruce stands at Ulborg than at the other sites indicate that differences in decomposition rate for Norway spruce may develop later on (Vesterdal and Raulund-Rasmussen 1997). In addition, macrofauna exclusion may to some extent have reduced differences in decomposition among the three soil types.

Conclusions

The experiment with beech litter supported the hypothesis that the rate of decomposition is influenced by soil type through its effect on both litter quality and the incubation environment. Beech litter mass loss was positively affected by nutrient status of the soil. The experiment with Norway spruce litter did not support the hypothesis as regards influence of soil type through the litter quality, and the effect through the soil environment was weak. Nutrient release from litter of both species was greatly affected by soil type through the litter quality, as the released amounts were positively related to initial nutrient concentrations. Nutrient release

was less affected by the soil environment. Soil environments only affected release of some nutrients, and the differences were not consistently related to nutrient status of soils or mass loss. The influence of soil nutrient status on decomposition appears to vary among tree species and may be more significant in species that produce relatively high quality litter.

Acknowledgements

The Danish Forest and Landscape Research Institute kindly allowed me to use the tree species trials for the experiment. I would like to thank Lena B. Troelsen for carrying out the nutrient analyses, and Peter Theis Hansen and Jens Holst-Nielsen for assistance with preparation of litterbags.

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Table 1. Physical and chemical characteristics of soils at the three sites.

Site	Depth (cm)	pH	Clay	Silt	Sand	C	N	P	Ca^{2+}	Mg^{2+}	K^{+}
			(%)			(%)	($mg \cdot g^{-1}$)	($mg \cdot kg^{-1}$)	($cmol_{+} \cdot kg^{-1}$)		
Christianssæde											
A1	0-5	3.8	12	10	78	2.8	2.1	110	4.6	0.6	0.12
A2	5-25	5.2	12	11	77	1.5	1.7	110	9.3	0.4	0.10
Bt	25-50	6.2	15	18	67	0.4	0.5	240	12.2	0.6	0.18
Btg	50-73	7.5	18	20	62			380	21.7	0.5	0.12
Ckg	73-110	7.7	9	16	75					0.3	0.07
Løvenholm											
A	0-27	4.1	3.5	12.0	85	0.9	0.7	119	0.47	0.06	0.06
Bw	27-55	4.8	2.5	6.5	91	0.4	0.3	161	0.48	0.05	0.04
BC	55-70	4.7	4.0	9.0	87	0.1	0.2	223	0.21	0.03	0.04
Cg	70-	4.5	3.5	10.5	86	0.1		123	0.78	0.07	0.07
Ulborg											
A	0-18	2.7	2.1	3.0	95	10.7	3.3	22	0.39	0.67	0.23
E	18-30	3.4	0.5	2.2	97	0.4	0.1	6	0.03	0.01	b.d.[a]
Bh	30-34	3.5	10.9	3.8	85	7.0	2.4	24	0.20	0.13	0.09
Bhs	34-40	4.1	6.2	3.6	90	3.6	1.3	20	0.06	0.04	0.04
Bs	40-60	4.4	2.9	3.0	94	0.1	0.1	16	0.02	b.d.	0.01
BC	60-100	4.5	1.3	2.1	97			10	0.01	b.d.	b.d.
C	100-	4.6	0.9	2.5	97			11	0.01	b.d.	b.d.

Note: From Raulund-Rasmussen (1993), Raulund-Rasmussen and Vejre (1995) and Vesterdal and Raulund-Rasmussen (1997).
[a]b.d.: below detection limit.

Table 2. Initial chemistry of beech and spruce litter from the three sites.

Species and site	Water						Ethanol		
	N	P	Ca	K	Mg	Mn	extract.	extract.	Lignin
	($mg \cdot g^{-1}$)						(%)		
Beech									
Christianssæde	11.7 (0.2)	1.19 (0.01)	17.3 (0.3)	4.97 (0.04)	2.09 (0.02)	0.41 (0.02)	10.2 (0.5)	5.4 (0.4)	34.3 (0.1)
Løvenholm	12.7 (0.4)	2.36 (0.07)	14.2 (0.7)	7.05 (0.24)	1.75 (0.05)	1.67 (0.01)	11.1 (0.9)	4.7 (0.4)	31.7 (0.1)
Ulborg	10.0 (0.2)	0.45 (0.02)	13.0 (0.7)	3.02 (0.12)	2.25 (0.01)	0.38 (0.00)	10.3 (0.1)	4.5 (0.2)	35.5 (0.3)
Norway spruce									
Christianssæde	10.5 (0.2)	0.93 (0.05)	16.6 (0.2)	2.21 (0.02)	0.95 (0.00)	0.89 (0.03)	7.1 (0.4)	5.1 (0.2)	36.8 (0.3)
Løvenholm	9.4 (0.2)	1.10 (0.03)	16.8 (0.3)	3.10 (0.01)	1.04 (0.00)	1.99 (0.08)	7.8 (0.5)	4.7 (0.3)	35.1 (0.1)
Ulborg	12.1 (0.2)	0.52 (0.00)	11.8 (0.1)	2.82 (0.01)	1.75 (0.01)	0.74 (0.04)	7.2 (0.4)	4.5 (0.3)	37.6 (0.1)

Note: Values are means (SD), n=3 for nutrient concentrations and n=2 for extractable organic fractions.

Table 3. Effects of incubation site, litter origin and time on mass loss in beech and Norway spruce litter through the entire period. *F* values from three-way analysis of variance.

	df	Beech	Norway spruce
Incubation site	2	19.8***	3.8*
Litter origin	2	137.5***	1.7 ns
Time	4	1282.0***	1300.0***
Inc. site × litter origin	8	1.3 ns	1.5 ns
Inc. site × time	8	11.5***	1.9 ns
Litter origin × time	8	3.1**	0.5 ns
Inc. site × litter origin × time	16	0.9 ns	1.1 ns

Note: df = degrees of freedom, *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns $p > 0.05$

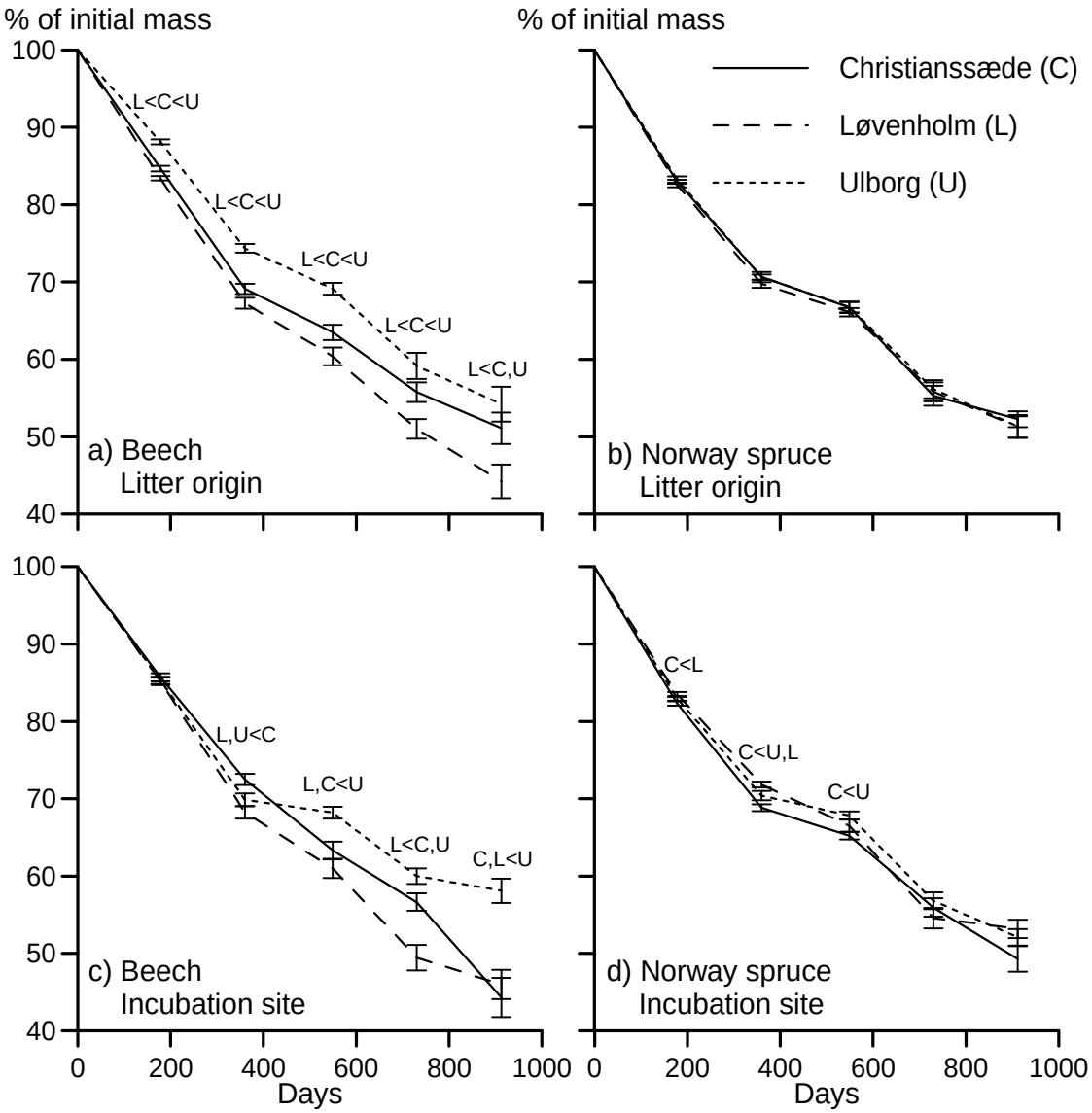

Fig. 1. Remaining mass of beech and Norway spruce foliage litter of different origin (a, b) and incubated at different sites (c, d). Bars indicate one standard error of the mean. At each sampling date, litter origins or incubation sites are ranked according to significant differences ($p < 0.05$) based on two-way analysis of variance. C, Christianssæde; L, Løvenholm; U, Ulborg.

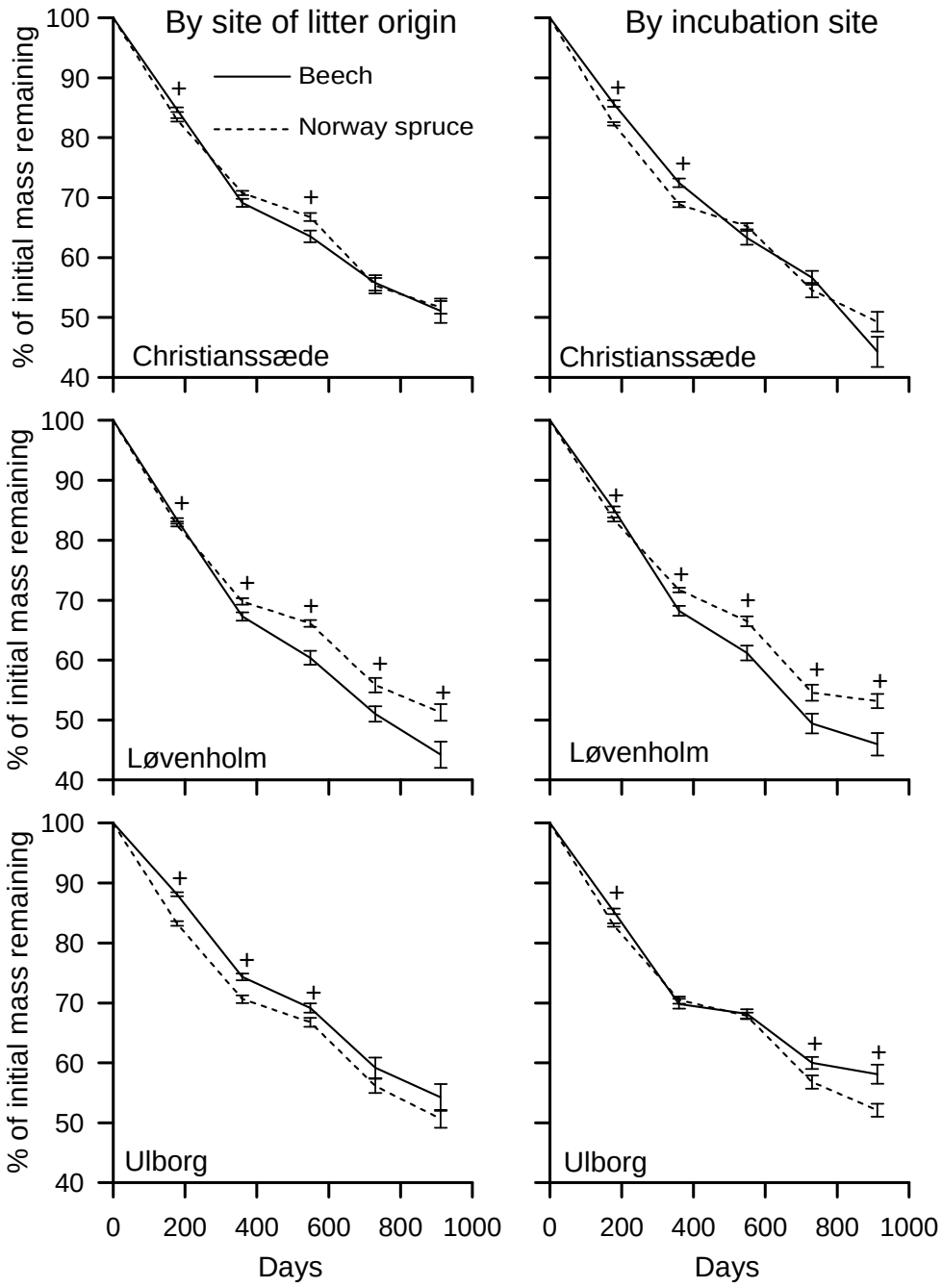

Fig. 2. Remaining mass of beech and Norway spruce foliage litter of the same origin (left column) and incubated at the same site (right column). Bars indicate one standard error of the mean. Significant differences ($p < 0.05$) between tree species at the individual sampling dates based on Student's *t* test are shown by +.

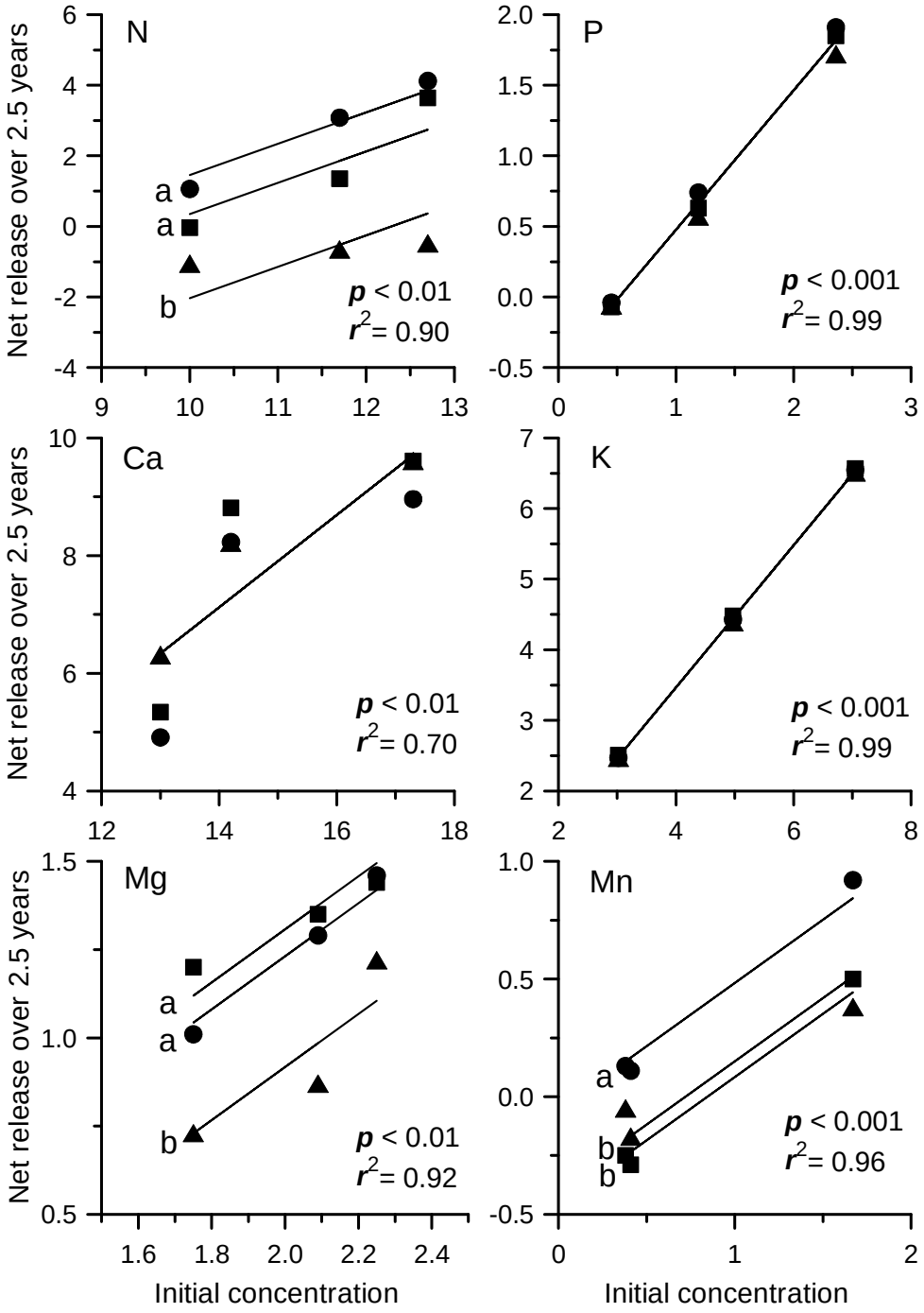

Fig. 3. Linear correlations between initial nutrient concentrations (mg·g^{-1}) and net nutrient release (mg·g^{-1} incubated litter) from beech leaf litter during 2.5 years incubation. Differences in nutrient release among incubation sites are indicated by individual regression lines. Lines with the same letter are not significantly different ($p > 0.05$) based on a general linear model and Student's *t* test. Incubation sites: ● Christianssæde, ■ Løvenholm, Δ Ulborg.

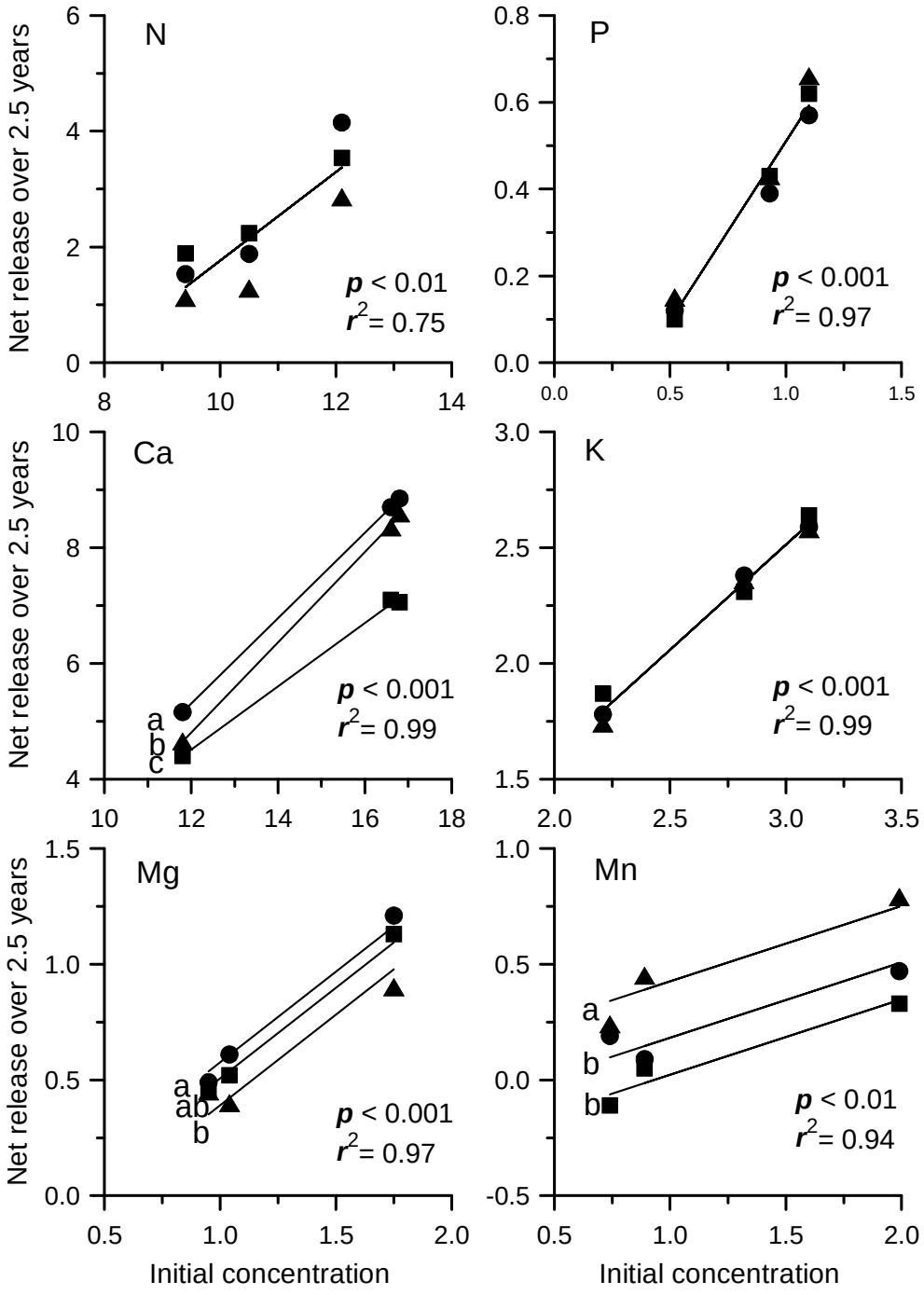

Fig. 4. Linear correlations between initial nutrient concentrations ($mg \cdot g^{-1}$) and net nutrient release ($mg \cdot g^{-1}$ litter) from Norway spruce needle litter during 2.5 years incubation. Differences in nutrient release among incubation sites are indicated by individual regression lines. Lines with the same letter are not significantly different ($p > 0.05$) based on a general linear model and Student's *t* test. Incubation sites: ● Christianssæde, ■ Løvenholm, Δ Ulborg.

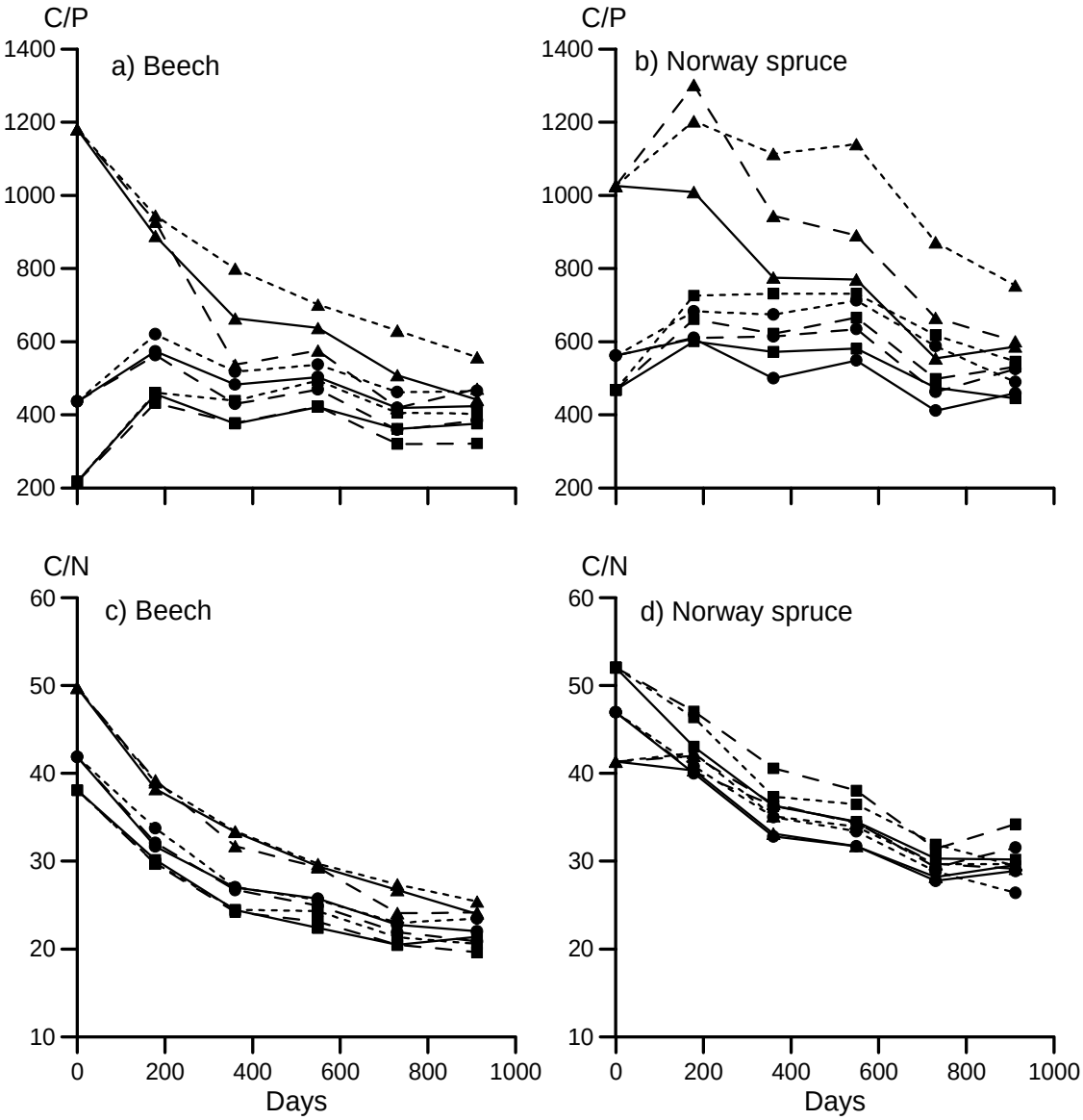

Figure 5. C/P ratios for beech (a) and Norway spruce (b), and C/N ratios for beech (c) and Norway spruce (d) through 2.5 years of decomposition. Litter of three origins: ● Christianssæde, ■ Løvenholm and Δ Ulborg, and incubated at three sites: ——— Christianssæde, -------- Løvenholm and ····· Ulborg.

Paper IV

Nitrogen cycling in coastal Douglas-fir forests along a gradient in soil nitrogen capital

Cindy Prescott, Nick Chappell and Lars Vesterdal

Ecology (submitted)

Running head: N cycling along a soil N gradient

NITROGEN CYCLING IN COASTAL DOUGLAS-FIR FORESTS ALONG A GRADIENT IN SOIL NITROGEN CAPITAL

Manuscript for Ecology.

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Abstract
Nitrogen cycling is generally considered to be more rapid on sites with inherently high availability of N. This study was conducted to determine whether N cycling in stands of a single tree species was affected by a gradient in mineral soil nitrogen capital. Rates of N cycling in stands of Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) were estimated by measuring annual N inputs in litter, accumulations of N in the forest floors and net N mineralization rates in the forest floors. Rates of N turnover were estimated from the litterfall/forest floor ratio. Nitrogen cycling increased along the soil N gradient due to increased N concentrations in litter and increased litterfall. Forest floor N contents decreased, and turnover rate constants of C and N indicated greater rates of decomposition and N release with increasing soil N capital. Carbon turnover was more affected than N turnover by soil N capital. Forest floor net N mineralization was poorly correlated with indices of N cycling, and forest floor C/N ratios did not reflect the changes in N cycling. For the most part, the results were consistent with the hypothesis that rates of N cycling within a single tree species increase with increasing soil N capital. The gradient in soil N capital may have developed from differences in rates of plant growth and organic matter production resulting from differences in soil texture among the sites.

Key Words: nitrogen cycling; Douglas-fir; soil nitrogen gradient; carbon turnover; nitrogen turnover; decomposition; net N mineralization; nitrogen availability; litterfall; forest floor;

Key Phrases: nitrogen cycling along gradient in soil N; effects on litterfall N content and C/N ratio; effects on C and N turnover and forest floor net N mineralization; net N mineralization vs. N cycling rates; positive feedback increasing N availability on N-rich sites vs. N-poor sites;

Introduction

It is generally considered that nitrogen cycling is more rapid on sites with inherently high availability of N. As Gosz (1981) outlined, vegetation on rich sites produces litter with high N concentrations and low amounts of phenolics, leading to rapid decomposition and mineralization of N. On N-poor sites, the litter has low N concentrations and higher amounts of phenolics, decomposes slowly and releases the N slowly. These differences in litter chemistry among sites thus create a feedback which increases N availability on rich sites but decreases it on poor sites. Support for this hypothesis has come from studies of N cycling along N availability gradients in Wisconsin. Pastor et al. (1984) reported higher litter N concentrations and faster decomposition and mineralization along a gradient in soil N mineralization. They attributed these effects to changes in species composition along the gradient, with species that produce higher quality litter replacing others as N availability increased. Differences in N mineralization were apparently the result of changes in soil texture; higher rates of soil N mineralization were associated with fine-textured soils with better moisture conditions. Similar conclusions were reached by Reich et al. (1997) who found correlations between N availability, aboveground net primary production and N return in litter along a more extensive N availability gradient in the same area. The differences in N availability were also associated with changes in the vegetation, and attributed ultimately to soil type, texture and parent material.

As most of the previous studies have dealt with gradients in N availability comprising different tree species, it is not clear to what extent the differences in N cycling also occur within single tree species. In loblolly pine (*Pinus taeda* L.), Birk and Vitousek (1986) found higher N concentrations and rates of N mineralization in stands with higher N availability, but this effect was largely a result of heavy fertilization with sewage sludge. Lamb (1975) found lower litter N concentrations, higher forest floor accumulation and slower N mineralization in radiata pine (Pinus radiata D. Don) plantations on poor sandy soils compared with richer sites. He attributed these effects to lower nutrient concentrations and higher concentrations of polyphenols in the litter on poor sites.

In this study we examined the influence of mineral soil N capital on rates of N cycling in coastal Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) at nine sites along a soil N gradient in Washington and Oregon. Rates of N cycling in the stands were estimated by measuring annual N inputs in litter, accumulations of N in the forest floors and rates of net N mineralization in the forest floors. Rates of N turnover were estimated from the litterfall/forest floor ratios. If Gosz's hypothesis applies to different sites with the same tree species, then rates of N input in litter, N turnover in the forest floor and net N mineralization would increase as soil N capital increased. The underlying causes of the differences in N capital among the sites were examined by comparing soil N capital with other site properties.

Materials and methods

Study sites

Nine coastal Douglas-fir stands of widely different site index were selected to represent a gradient in N availability, based on the established relationship between N availability and productivity in Douglas-fir (Chappell et al., 1991). Eight stands were located in coastal Washington and one was in coastal Oregon. The stands were fully-stocked second growth and were control plots in a fertilization trial established 1969/70 as part of Phase I of the Regional Forest Nutrition Research Project (now the Stand Management Cooperative (SMC)). Age, stem number, and standing volume varied among the stands (Table 1). Parent material also varied as five of the sites had soils developed from glacial till or glacial sediments and the others had soils developed from igneous and sedimentary rocks. Soil properties for the surface 15 cm layer are given in Table 2 together with total contents of C and N in the soil profile. The soils were fairly rich in clay and silt except for Skykomish and White Chuck Mountain, and pH was fairly uniform among the sites (4.2-5.4 for the entire profile). The variations in cation exchange capacity and base saturation were small, but C, N, and P concentrations of the mineral soils varied among the sites. Total C and N contents in the soils are from profiles ranging from 63 to 152 cm in depth. The differences in profile depth were not related to soil C and N capitals and were assumed to be of little importance due to very low concentrations in the deep soil horizons.

Sampling and analyses

The rate of N cycling in each stand was estimated by measuring: 1) N concentration in needle litter and annual litterfall mass, 2) N concentration and mass of the forest floor, and 3) net N mineralization in the forest floor. All sampling was done within the 0.04 ha measurement plot in each stand.

To estimate the N content of litterfall, ten 0.135 m^2 plastic trays with fiberglass screens in the bottom and holes for drainage were randomly placed in each measurement plot in April 1993. Fallen litter was collected from each tray at two-month intervals for one year, dried at 70°C, sorted into brown needles, green needles and other material, and weighed. Only brown needles having undergone senescence and abscission were measured since these would best represent the nutritional conditions of the site. Green needles were excluded because they were mostly attached to branches broken off during windstorms. Concentrations of C and N were measured in litter collected in October following the annual peak in litterfall, using a CHN analyzer (Perkin Elmer Series II CHNS/O Analyzer 2400, Perkin Elmer, Norwalk, CT). The total amounts of C and N in annual litterfall were estimated by multiplying the mass of litter in each tray by the concentrations of C and N.

The mass of the forest floors were estimated from five 0.093 m^2 samples of the Oi, Oe, and Oa layers collected from each plot in October 1993. Samples were dried at 70°C and woody debris larger than 1 cm in diameter was removed. The remaining material was weighed, and

concentrations of total C and N were measured with the CHN analyzer. The total amounts of C and N in the forest floors were estimated by multiplying the masses of the forest floors by the concentrations of C and N.

Forest floor turnover rates were calculated for both C and N by the litterfall/forest floor mass ratio according to Olson (1963). Turnover estimates were based on brown needle litter and all forest floor material except woody debris larger than 1 cm. Estimates are thus primarily suitable for comparison among the nine stands. The assumption of the stands being in steady state, i.e. that annual forest floor decomposition in the forest floor equaled annual litterfall, was not tested. However, since all stands were more than 40 years old they should be approximating steady state conditions. There would be no residual forest floor material from the previous stands, so forest floor masses should reflect rates of litter production and decomposition in the current stands. Because the stands closed canopies many years earlier, rates of litter production should have stabilized. Average forest floor masses may have been slightly overestimated by sampling shortly after the annual litterfall peaks so turnover rates may have been slightly underestimated.

Potential rates of net N mineralization in the forest floor were estimated from the amounts of NH_4-N and NO_3-N produced during 24-day aerobic incubations in the laboratory (Vitousek et al., 1982). Ten samples of the Oe and Oa layers in each plot were collected in October 1993 separately from the forest floor mass samples described above. A 5 g subsample (dry weight equivalent) was extracted with 2M KCl and concentrations of NH_4-N and NO_3-N were measured on an Alpkem RFA 300 AutoAnalyzer (Alpkem Corp., Wilsonville, OR; Page et al., 1982). A second 10 g subsample (dry weight equivalent) was placed in a 0.6 dm^3 glass jar. Distilled water was sprayed into each subsample to bring the moisture contents to 75% (wet weight basis), and the jars were incubated in the dark at about 20°C. Each week, the jars were opened to outside air for 15 min. After 24 days, each sample was extracted with 2M KCl. Differences between the amounts of extractable N before and after incubation were used to estimate net N mineralization rates in each forest floor sample.

Data analysis

Correlations between soil N capital and rates of N cycling were tested by linear regression with PROC GLM (SAS, 1989). Intercorrelation between soil N capital and other site characteristics were tested using correlation analysis (PROC CORR) and subsequent linear regression.

Results

Litterfall and forest floor C and N for the nine stands are shown in Table 3 together with the estimated turnover rate constants. Litterfall C and N contents increased significantly, and litterfall C/N ratio decreased significantly along the gradient in soil N capital (Figs. 1a-c). These relationships indicated that stands with low litterfall N contents might also produce the

most N-poor litter. There was a tendency for stands with low litterfall N content to produce the most N-poor litter, but the correlation was not quite significant (Fig. 1d).

Forest floor C and N contents tended to decrease along the soil N gradient, but only the relationship between forest floor N content and soil N was significant (Figs. 2a-b). Turnover rate constants of C and N both increased significantly along the soil N gradient (Fig. 3), suggesting faster decomposition with increasing amounts of soil N. Since the variation in forest floor C and N contents along the soil N gradient was fairly small, the variation in C and N turnover constants was largely the result of the differences in litterfall C and N contents. Nitrogen turnover did not increase to the extent that C turnover increased along the soil N gradient, despite an increase in litterfall N concentration. Thus, N turnover appeared to be less affected by soil N than C turnover, as the slopes of the regression lines were significantly different ($P<0.05$).

Forest floor net N mineralization was highest at the two sites with lowest forest floor C/N ratios, and mineralization was generally low above a C/N ratio of 35 (Fig. 4). However, net N mineralization was not correlated with either soil N capital, litter N content, or litter C/N ratio. The increasing N content and N concentration in litterfall along the gradient was apparently not reflected in the forest floor C/N ratio (Fig. 5). Surprisingly, there was an inverse relationship between forest floor N concentration and soil N.

The relationships between soil N capital and soil properties listed in Table 2 were explored in order to identify other site factors associated with soil N. Soil N was significantly positively correlated only with soil C ($P<0.05$, $r^2=0.61$), and soil C was also significantly positively correlated with both litter N concentration ($P<0.05$, $r^2=0.52$) and litter N content ($P<0.05$, $r^2=0.61$). Soil C/N was not correlated with litter N content ($P=0.07$) or litter C/N ratio ($P=0.19$). Turnover rate constants were negatively correlated with mineral soil C/N (Fig. 6). None of the other site and soil properties listed in Tables 1 and 2 were significantly correlated with either soil N capital or turnover rates. However, percentage clay (0-60 cm depth) was correlated with soil carbon content ($P<0.05$) (Fig. 7). This suggests that the effect of the soil N gradient might be associated with a soil textural gradient, although the correlation between soil N and percentage clay was not significant ($P=0.10$).

Discussion

The results of this study are for the most part consistent with the hypothesis that rates of N cycling would increase along the gradient in soil N. The amount of N returned in litter and the rate of N turnover in the forest floor both increased as soil N capital increased. The increase in litter N content resulted from both increased litter mass and increased N concentrations in litter. Increasingly N-rich litter with increasing litterfall N content (Fig. 1d) was also reported by Vitousek et al. (1982) from sites with different tree species. Despite the increase in litter input, forest floor mass declined along the gradient, suggesting a faster decomposition on

more N-rich sites. As suggested by Gosz (1981) this may be due to higher concentrations of N and lower concentrations of polyphenols in litter. Litterfall C/N ratio was lower on the more N-rich sites, but preliminary analyses of condensed tannins in litterfall did not suggest declining contents of polyphenols along the gradient (K. Venner, personal communication).

Correlations between litterfall nitrogen content and net N mineralization as the index of soil N availability have also been reported from other studies (Pastor et al., 1984; Reich et al., 1997). However, these studies had soil N gradients made up by different tree species. Within a tree species, Birk and Vitousek (1986) found that increased N availability was related to increased litterfall and increased concentrations of N in litterfall. Turnover rate constants for C and N also increased along the soil N gradient suggesting faster decomposition and N release. McClaugherty et al. (1985) also reported higher decomposition rates on N-rich sites, but this effect was due to changes in tree species. Within a species, effects of N availability on decomposition have been inconsistent (Fog, 1988). Cotrufo et al. (1995) reported slower decomposition of birch leaf litter with increasing C/N ratios, whereas Prescott (1995) found no change in decomposition rates of litter enriched with N. Aerts and De Caluwe (1997) also reported little influence of litter N concentrations on decomposition rates within Carex species. However, they found that N release was highest under conditions of high N supply, as also indicated by the increasing N turnover rate along the soil N gradient in our study.

We found only found poor correlations between forest floor net N mineralization and indices of N cycling rates. The only exception was the higher net N mineralization at the two sites with forest floor C/N ratios below 35. Other studies by Lamb (1975) and Vitousek et al. (1982) also found no correlation between mineralization and forest floor C/N ratio, but they found litter N content to be a better predictor of N mineralization. In our study litter N content was not correlated with forest floor net N mineralization, in fact there was a tendency for higher N mineralization with higher litter C/N ratio. This resulted from an unexpected negative relationship between N concentrations in litter and forest floors - sites with the highest C/N ratios in litter had the lowest C/N ratios in the forest floor. Such a pattern could be related to higher polyphenol concentrations in litter and greater complexing of proteins in the forest floor at sites with low soil N (Gosz, 1981). As a result, more of the N would be retained in the forest floor, causing a narrower C/N ratio. For this reason, the C/N ratio of the forest floor may not be a reliable predictor of site N availability.

Our results provide further evidence of a positive feedback that increases N availability on N-rich sites and decreases N availability on N-poor sites. The question remains, what are the site factors that initially determine N availability? Gosz (1981) suggested that the nature of the parent material, particularly texture and nutrient status would influence N cycling by determining plant development. Under similar climatic conditions, soils with favorable moisture capacity and adequate amounts of nutrients will result in greater productivity, biomass, organic matter storage and N supply. Reich et al. (1997) demonstrated a relationship

between net primary productivity and net N mineralization, both being higher on fine-textured Alfisols than on more coarse-textured Entisols, Histosols, and Spodosols. Lamb (1975) found lower rates of N cycling in radiata pine stands on sandy podzols than on more fine-textured soils. We could not find any differences in soil nutrients among the nine sites that were able to explain the variation in N cycling. There was, however, a positive correlation between soil C and percentage clay in 0-60 cm depth ($P<0.05$) and a weaker, non-significant relationship between soil N and percentage clay ($P=0.10$). The soil N gradient may therefore be a result of differences in soil texture among the sites, according to the following scenario. At the sites with fine-textured soils, the higher moisture holding capacity and higher content of base cations would promote plant growth and production of organic matter. Over time these sites would develop higher contents of organic matter, C, and N in the soil. The feedback through increased litter N contents identified in this study would further increase turnover and N availability at the N-rich sites. On the coarse-textured soils organic matter, C, and N would accumulate more slowly, being further constrained by slower N cycling in litter.

In conclusion, our results were for the most part consistent with the hypothesis that rates of N cycling would increase along the gradient in soil N. The amounts of N returned in litter and the rate of N turnover both increased with increasing soil N capital. Turnover rate constants also increased along the soil N gradient. However, forest floor net N mineralization was not clearly related to indices of litter N cycling, and forest floor C/N ratio did not reflect litter N cycling. The study provided further evidence of a positive feedback increasing N availability on N-rich sites and decreasing N availability on N-poor sites. Differences in soil texture among the sites may be partly responsible for the development of differences in soil N capital and the resulting patterns of N cycling.

Acknowledgments

The support of Stand Management Cooperative member organizations and the Natural Sciences and Engineering Research Council of Canada is gratefully acknowledged. We thank D. Bradley, R. Gonyea, B. Hasselberg, M. Holmes, C. Staley, and K. Thomas for field and laboratory assistance.

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Table 1. Site and stand characteristics at the time of sampling in 1993.

Site†	Soil suborder (USDA)	Parent material	Aspect	Slope (%)	Elevation (m)	Precipitation (cm)	Age (yr)	Site index (m)	Stem number (ha^{-1})	Volume (m^3/ha)	Annual increment‡ ($m^3\ ha^{-1}\ yr^{-1}$)
Skykomish (43)	Haplorthod	Granite	NW	10	457	-	70	26	1960	923	18.4
White Chuck Mountain (110)	Fragiorthod	Meta-igneous shale	SE	60	945	292	42	35	1235	672	26.6
Cedar Falls Powerline (5)	Xerochrept	Glacial till	E	10	274	178	62	31	872	613	13.7
Cedar Falls (1)	Durochrept	Glacial till	level	5	344	203	67	35	472	781	11.8
Little Ohop Creek (17)	Haploxeralf	Sandstone	SE	20	671	152	51	40	1111	944	20.7
Headquarter Camp (57)	Haplohumult	Igneous	level	10	536	165	59	40	474	1018	23.0
Middle Fork Satsop River (77)	Haplorthod	Glacial till	level	10	162	229	46	38	1383	613	24.4
Deep Creek (20)	Haplumbrept	Glacial sediments	SE	10	373	178	56	42	630	844	16.8
Camp Grisdale (53)	Haplumbrept	Glacial till	W	15	421	292	52	37	751	878	24.6

† Stand Management Cooperative installation numbers in brackets.

‡ Annual increments are for the previous 24-year period except for Middle Fork Satsop River where stocking characteristics are from 1989 and annual increment is for 1969-1989.

Table 2. Selected properties of soils at the nine sites. Texture, pH, cation exchange capacity (CEC), base saturation (BS), total P, available P (Bray), and C and N concentrations are based on four composite samples from the upper 15 cm in each stand. Total C and N are gravel-corrected contents in the whole mineral soil profile.

Site	Clay (%)	Silt	Sand	pHH_20 ($cmol_+/kg$)	CEC (%)	BS	Total P (mg/kg)	Bray P (%)	C (%)	N	Total C (Mg/ha)	Total N
Skykomish	6	10	84	5.0	20.8	9.4	672	58	3.25	0.09	83	2.53
White Chuck Mountain	5	15	80	4.7	21.8	21.9	1084	162	4.04	0.12	84	3.28
Cedar Falls Powerline	13	37	50	-	33.8	13.5	2078	174	4.52	0.16	91	4.06
Cedar Falls	11	26	63	4.9	40.4	18.3	2306	156	9.71	0.41	108	4.50
Little Ohop Creek	30	50	20	5.0	38.3	13.2	372	4	5.51	0.19	220	7.00
Headquarter Camp	20	40	40	5.2	30.4	7.9	1340	43	4.45	0.22	141	8.50
Middle Fork Satsop River	10	25	65	5.0	22.5	14.8	1811	105	9.28	0.40	173	9.68
Deep Creek	30	37	33	5.1	26.1	27.1	1179	113	4.07	0.21	143	10.54
Camp Grisdale	20	50	30	4.6	40.1	5.4	1124	9	7.83	0.32	208	12.10

Table 3. Carbon and nitrogen contents of litterfall and forest floors, net N mineralization in forest floors, and turnover rate constants for carbon and nitrogen at the nine sites. Each value is the mean (and standard error) of 10 samples per site for litterfall and net N mineralization or 5 samples per site for forest floors.

Site	Litterfall			Forest floor				Turnover†	
	Carbon	Nitrogen	C/N	Carbon	Nitrogen	C/N	N min	C	N
	($kg\ ha^{-1}\ yr^{-1}$)			(Mg/ha)	(kg/ha)		($\mu g\ g^{-1}\ d^{-1}$)		
Skykomish	584 (119)	5.04 (1.25)	110	6.13 (0.59)	170.6 (16.4)	36	8.3 (0.9)	0.10	0.03
White Chuck Mountain	709 (133)	6.92 (1.52)	100	3.49 (0.18)	102.8 (7.8)	34	45.5 (18.3)	0.20	0.07
Cedar Falls Powerline	457 (65)	5.57 (0.92)	82	4.28 (0.65)	124.8 (12.0)	34	22.6 (4.6)	0.11	0.04
Cedar Falls	457 (69)	5.60 (1.09)	82	2.98 (0.29)	79.7 (6.3)	37	5.4 (1.8)	0.15	0.07
Little Ohop Creek	730 (100)	9.05 (1.57)	79	4.33 (2.19)	110.4 (52.4)	39	0.4 (0.3)	0.17	0.08
Headquarter Camp	740 (115)	9.04 (1.54)	82	2.65 (0.32)	63.5 (6.1)	42	5.5 (1.2)	0.28	0.14
Middle Fork Satsop River	921 (121)	12.82 (1.89)	73	3.24 (0.20)	84.2 (5.7)	38	0.9 (0.8)	0.28	0.15
Deep Creek	1096 (77)	12.45 (1.07)	92	3.57 (0.40)	90.3 (5.7)	40	6.9 (1.5)	0.31	0.13
Camp Grisdale	1171 (93)	16.26 (1.96)	70	2.90 (0.32)	76.5 (7.7)	38	1.4 (0.2)	0.40	0.22

† Estimated proportion of forest floor C and N decomposed each year.

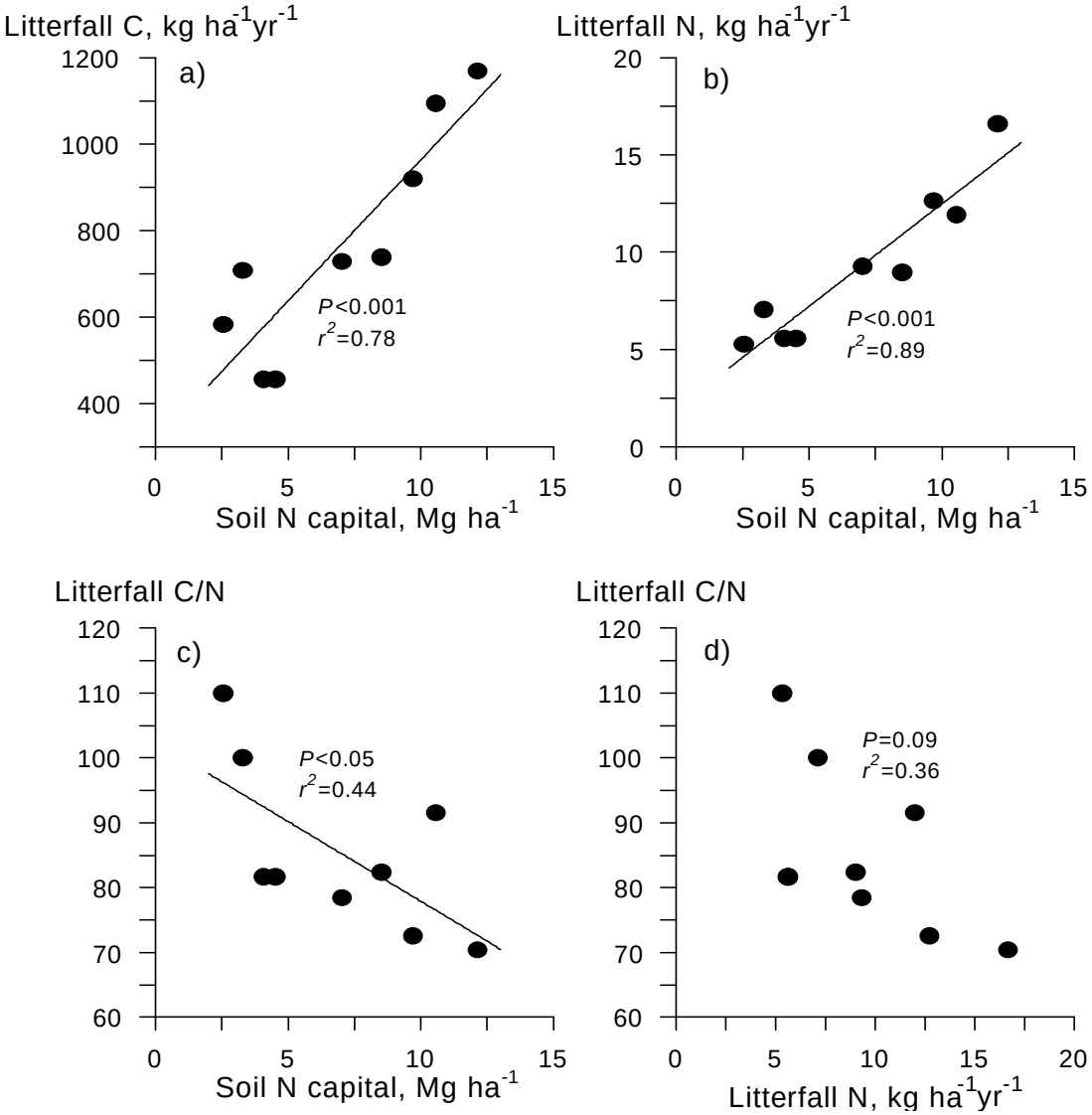

Fig. 1. Aboveground litter inputs along the gradient in soil nitrogen capital: a) litterfall carbon content, b) litterfall nitrogen content, c) litterfall C/N ratio, and d) litterfall N content and litterfall C/N ratio.

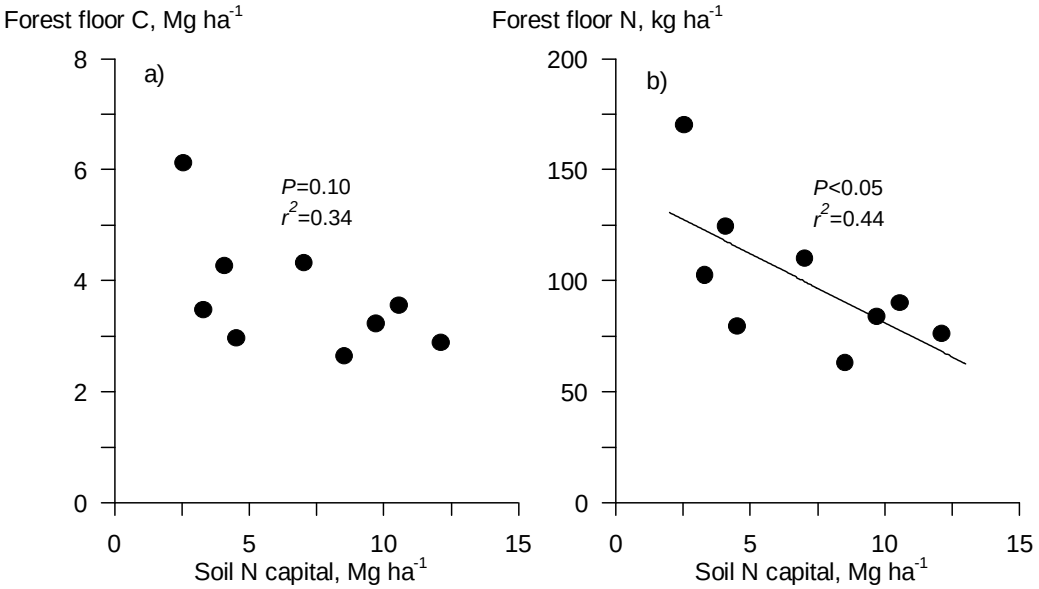

Fig. 2. Forest floors along the gradient in soil nitrogen capital: a) carbon contents, and b) nitrogen contents.

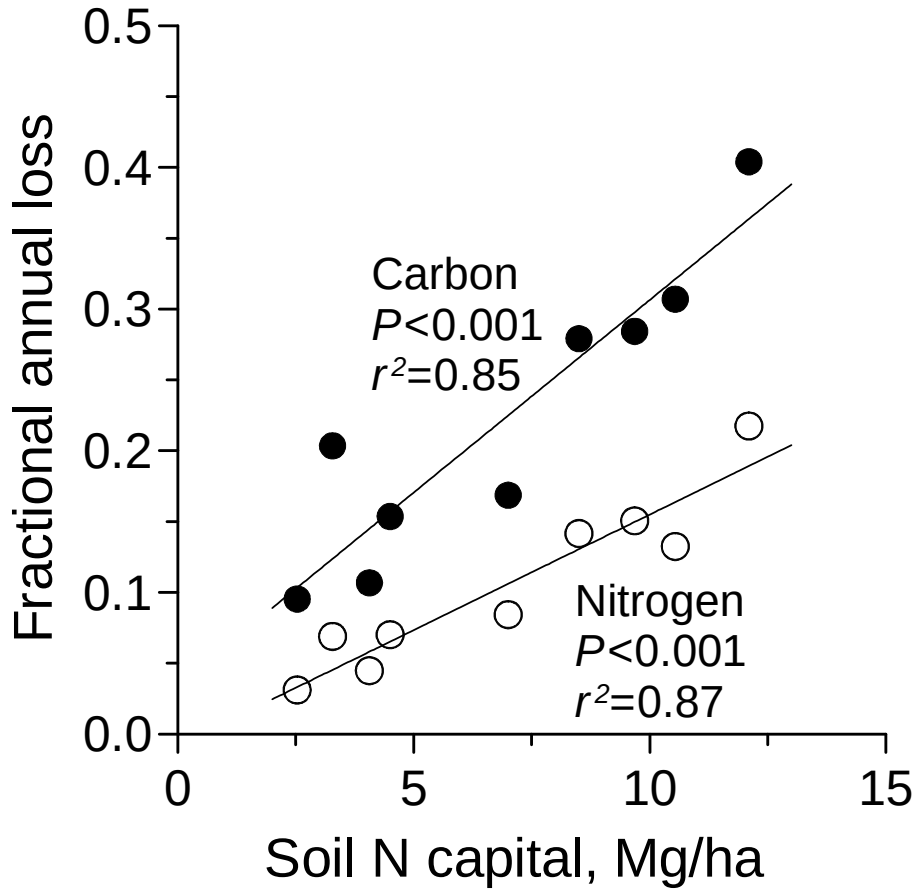

Fig. 3. Turnover rate constants (k) for carbon and nitrogen along the gradient in soil N capital. The slopes of the regression lines are significantly different (P<0.05).

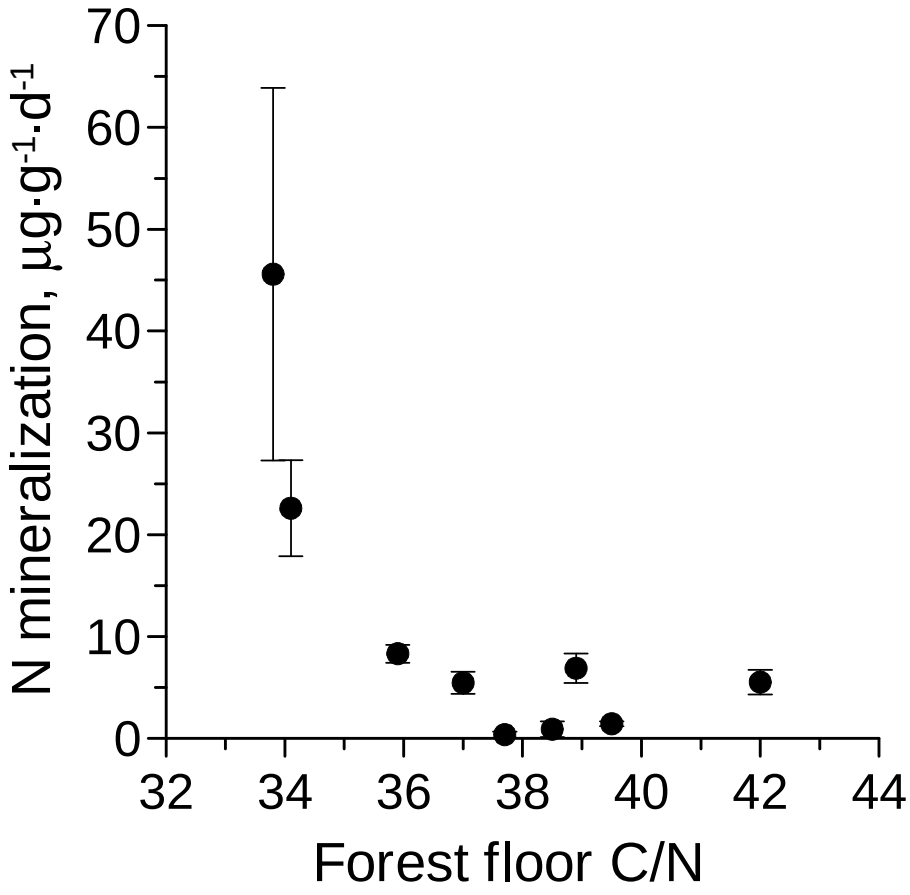

Fig. 4. Forest floor C/N ratios and net N mineralization rates during a 24-day laboratory incubation. Bars indicate standard errors.

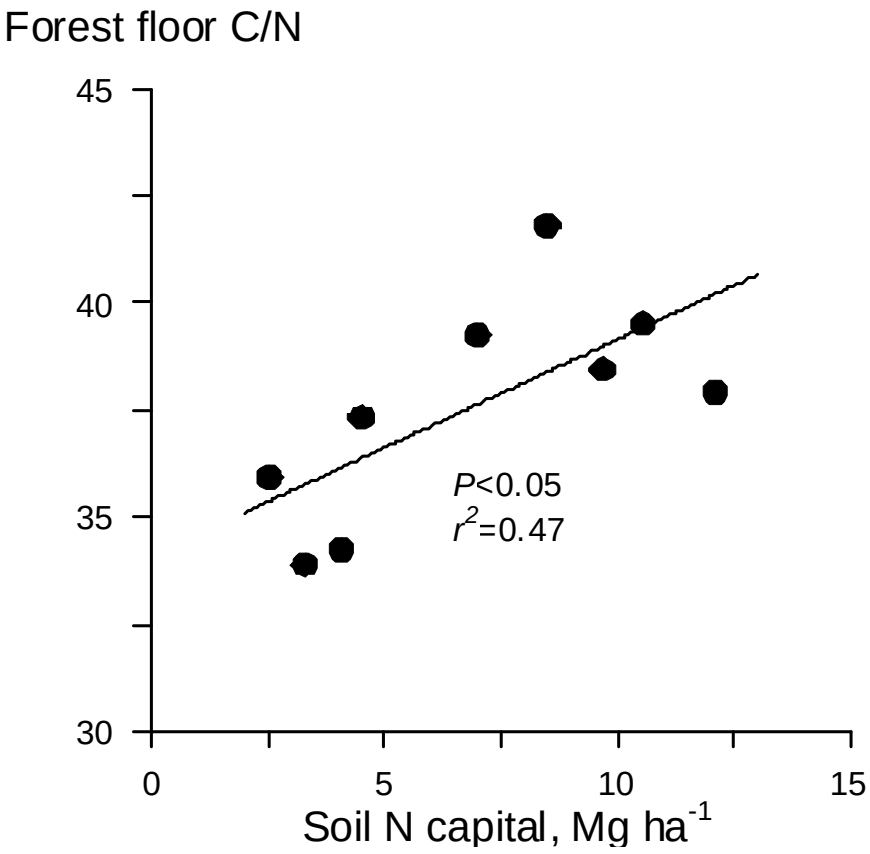

Fig. 5. Forest floor C/N ratios along the gradient in soil N capital.

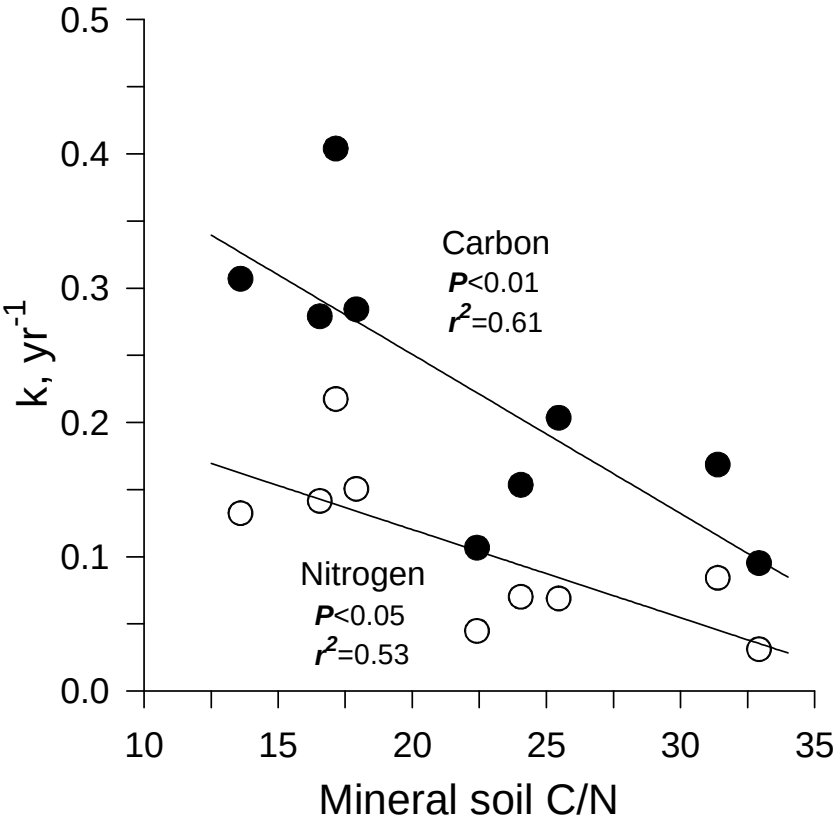

Fig. 6. Turnover rate constants (k) for carbon and nitrogen along a gradient in mineral soil C/N ratio.

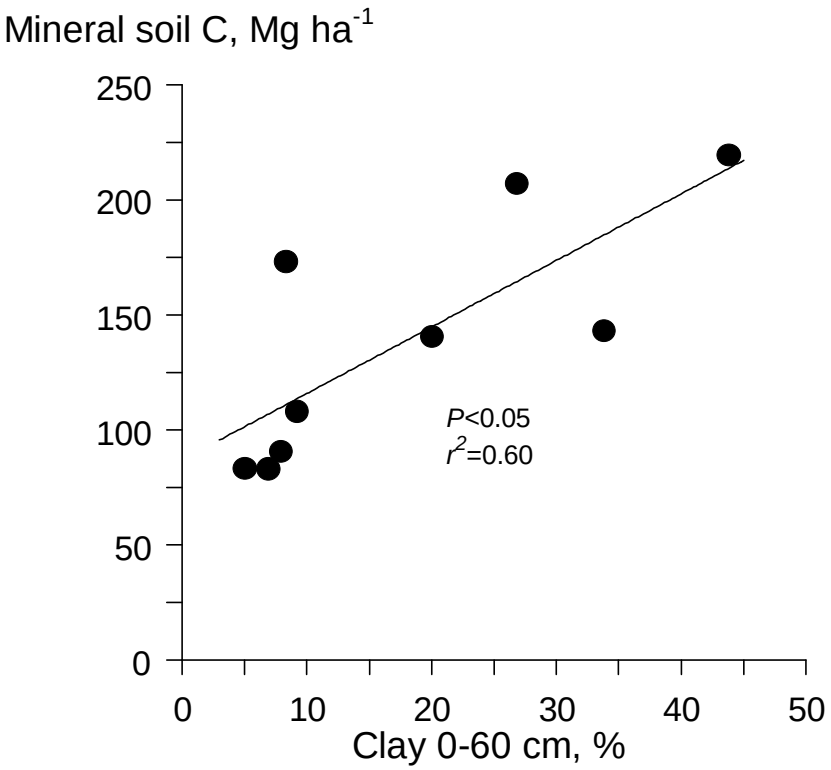

Fig. 7. The relationship between mineral soil carbon content and horizon-weighted percentage clay in 0-60 cm depth.

Paper V

Potential microbial nitrogen and phosphorus availability in forest floors

Lars Vesterdal

Soil Biology & Biochemistry (submitted)

POTENTIAL MICROBIAL NITROGEN AND PHOSPHORUS AVAILABILITY IN FOREST FLOORS

Short title: Microbial N and P availability in forest floors

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Summary—The potential availability of nitrogen and phosphorus to microorganisms in forest floors was studied by means of a bioassay. Microbial N and P availability was assessed by analysing the respiration rate response to addition of different amounts of N and P when glucose and other nutrients were added in excess. Forest floors of Norway spruce, Sitka spruce, Douglas-fir, beech, and oak from three sites of different nutrient status were studied. Oak forest floors had higher microbial N and P availability than forest floors of the other species, and P availability was lowest in Norway spruce forest floors. Sites differed only slightly in microbial P availability. The site with the most P rich soil also had the highest P availability in forest floors. The microbially available proportion of total P was very high, and much higher than the available proportion of total N. Microbially available N was not related to KCl-extractable N, total N concentrations or C/N ratios, nor was microbially available P related to concentrations of total P or C/P ratios. Basal respiration rates were related to microbial N and P availability. The bioassay assessed simple organic N compounds fairly well when added to forest floor material in low amounts. Microbial N and P availability in forest floors may be more dependent on other quality parameters than total N and P concentrations, e.g. the organic forms of N and P.

INTRODUCTION

Availability of nitrogen and phosphorus in the forest floor, i.e. the layer of more or less decomposed organic matter above the mineral soil, is an important factor for microbial activity (Stotzky and Norman, 1961; Tewary *et al.,* 1982; Christensen *et al.,* 1996), and in the end for decomposition rates (Enriquez *et al.*, 1993). Different methods have been introduced in order to characterize N and P availability by means of an adequate index (Binkley and Vitousek, 1989; Binkley and Hart, 1989). Although many attempts have been made to develop methods which extract biologically available fractions of N and P by use of a chemical extraction procedure, such indices are often doubtful as measures of the biologically available fractions. As discussed by Chapin *et al.* (1986), nutrient availability may be viewed in two ways: Either as the rate at which the soil supplies living organisms with accessible nutrients, or as the extent to which biological activity is limited by nutrient supply. Whereas the traditionally used extraction methods assess the ability of soils to supply nutrients, bioassays assess nutrient availability as a function of nutrient limitation by using the response of plants or microorganisms. Bioassay approaches have been used for studying plant available N and P in forest floors (Van Cleve *et al.*, 1986; Prescott *et al.*, 1993), and Scheu and Parkinson (1995) assessed the nutrient status of microbial biomass using the respiratory response to nutrient addition. A bioassay for estimation of microbially available N and P in forest floors was developed by Nordgren (1992). This bioassay is based on the respiration response of forest floor samples treated with glucose and nutrients. Experiments performed by Drobnik (1960), Stotzky and Norman (1961), Anderson and Domsch (1978), Nordgren *et al.* (1988) and Christensen *et al.* (1996) have all shown microbial respiration rate response to additions of glucose or glucose together with different amounts of N and P. When forest floor material is supplied with glucose and other nutrients in excess, the respiration rate response will be in proportion to the added amount of N. This principle was used by Nordgren (1992) to assess the N and P pools originally available to microorganisms in forest floor material from a single stand. It was possible to determine different levels of available N corresponding to different levels of mineralized N after incubation periods of varying duration.

The aim of this study was to examine if the bioassay could detect differences in potential microbial N and P availability in forest floors which were related to tree species and nutrient status of sites. Further, the ability of the bioassay to assess N was examined by addition of simple organic N compounds to forest floor material. Bioassay results were compared with results from N extraction and chemical analysis to investigate the relations to more conventional measures of N and P availability.

MATERIALS AND METHODS

Tree species and sites

Even aged monoculture stands of five tree species at three sites were included in the study. The tree species were beech (*Fagus sylvatica* L.), common oak (*Quercus robur* L.), Norway spruce (*Picea abies* (L.) Karst.), Sitka spruce (*Picea sitchensis* (Bong.) Carr.), and

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). The three sites are part of a tree species trial established by The Danish Forest and Landscape Research Institute in 1964/65. The sites differed in soil nutrient status (Raulund-Rasmussen, 1993). The site Frederiksborg (Typic Argiudoll) had a loamy parent material, whereas the sites Ulborg (Typic Haplohumod) and Lindet (Typic Quartzipsamment) had sandy parent materials. The climate was fairly similar among the sites: Mean annual precipitation 860-890 mm and mean annual temperatures 7.5-7.7°C (Danish Meteorological Institute). Forest floors at Frederiksborg were thin and mull-like, whereas forest floors at Lindet and Ulborg were thick and mor-like. Selected data for forest floors and mineral soils are given in Table 1.

Sampling and preparation

Sampling was carried out after removal of newly shed litter in the forest floor, and samples thus consisted of partially decomposed materials (F and H layers). Four subsamples from each stand were pooled to form one composite sample. The samples were brought to the laboratory for mixing, and larger roots, twigs, and fruits were excluded. The moisture contents of the samples were adjusted to 250% of dry weight in order to create optimal and equal growth conditions for microorganisms (Nordgren *et al.*, 1988). This was done either by addition of demineralized water, or by drying at room temperature while mixing frequently in order to avoid surface drying. The samples were stored at 4°C prior to incubation. NH4,+-N and NO3,--N were measured by flow injection analysis after extraction with 1 M KCl (in other respects according to Keeney and Nelson (1982)). Unfortunately, total N and P concentrations were not determined on the sampled FH material. Data on total N and P concentrations for pooled forest floor material (i.e. including the recently fallen litter) were used as a substitute. Total N and P concentrations may have been slightly higher in the FH material than in the pooled material (Alban, 1982).

Bioassay

The bioassay experiments were carried out with a respirometer described by Nordgren (1988, 1992). The respiration measurements are based on conductivity changes when CO_2 is trapped in a KOH solution. The bioassay for available N was carried out according to Nordgren (1992) by adding glucose (0.4 g) and P (2.3 mg P as KH_2PO_4) in surplus to 4 g ww forest floor material together with six levels of N (0-2.5 mg N as $(NH_4)_2SO_4$). Available P was determined by adding glucose and N in surplus (22 mg N as $(NH_4)_2SO_4$) with six levels of P (0-0.5 mg P as KH_2PO_4). Every combination was replicated five times. Further, ten replicates of each forest floor sample were incubated without any additions to measure basal respiration rates.

Urea, glycine, and glutathione were added separately to forest floor material from Norway spruce at Frederiksborg in order to test the estimate of N availability. Two levels of each organic N compound (0.45 and 0.90 mg N g^{-1} dw organic matter) were added before carrying out the bioassay.

Calculation of microbilally available nitrogen and phosphorus

The amounts of available N and P were estimated from linear regressions of "limited respiration rate" against the added amounts of N and P, respectively (Nordgren, 1992). The limited respiration rate is the maximum respiration rate attained due to vigorous reproduction of the microbial population after addition of glucose and nutrients. The limited respiration rates were linearly correlated with the added amounts of N and P ($P < 0.001$) for all forest floor samples. Figure 1a shows examples of respiration curves after different N additions, and Fig. 1b shows the resulting regression between limited respiration rates and added N. As discussed by Nordgren (1992), estimation of microbially available N and P may be done in two ways. One method is to extrapolate the regression line to an intercept with the x-axis (corresponding to no respiration). The numerical value of the x intercept then represents the potential amount of the nutrient initially available. This method assumes that linearity also applies to this availability regime, and is subsequently referred to as uncorrected availability. The other method defines microbial availability only as the amounts contained in the newly formed biomass as it is uncertain whether the native biomass reflected in the substrate induced respiration rate (SIR) had the same nutrient concentration. SIR was defined as the stable respiration rate attained immediately after start of the experiment (Fig. 1a) (Nordgren *et al.*, 1988). The regression line is therefore extrapolated only to the respiration rate level of SIR and this estimate is subsequently referred to as SIR corrected availability. Both availability indices were included in this study, as they may be regarded as maximum and minimum values, respectively, until it is possible to decide which is preferable (Nordgren, 1992).

Statistical analysis

Effects of tree species and sites on N and P availability and basal respiration rate were tested in SAS (SAS Institute, 1993) by one-way ANOVA using site as block factor. Nitrogen and P availability data were log transformed prior to statistical analysis in order to homogenize variances. In case of significant effects, Duncan's multiple range test was used to compare tree species and sites. All linear correlations were tested with the procedure REG.

RESULTS

Nitrogen availability

Figure 2 shows that oak forest floors had a high microbial N availability whereas Norway spruce had the lowest N availability. The uncorrected and SIR corrected availability indices were significantly affected by tree species ($P < 0.01$ and $P < 0.05$, respectively) (Table 2), and the uncorrected N availability was significantly higher in oak forest floors than in forest floors of all other tree species (Table 2). The SIR corrected N availability was significantly higher in oak than in beech, Sitka spruce, and Norway spruce.

The SIR corrected N availability indices were closely related to the uncorrected N availability ($P < 0.001$, $r^2 = 0.58$). The two availability indices for beech and oak at Frederiksborg differed more than for other samples (Fig. 2), and the correlation was improved

when these results were excluded ($P < 0.001$, $r^2 = 0.90$). SIR corrected N availability was on average 69 % (range 44-88 %) of the uncorrected N availability (75% and range 53-88% without beech and oak at Frederiksborg).

The amount of N extracted with KCl was generally lower than the amount of available N obtained with the bioassay (Table 3), and there was no correlation between results from the two assays. The potentially available amount of N estimated by the bioassay was much lower than the total amount of N in all forest floors. The available percentage of total N tended to be lowest at Lindet, where differences among tree species also were small. At Frederiksborg and Ulborg, Douglas-fir and oak had fairly high available proportions of the total N concentrations. Total N concentrations were not significantly correlated with the N availability indices obtained with the bioassay. SIR corrected N availability tended to be negatively correlated with forest floor C/N ratios, but the correlation was not significant ($P = 0.14$).

The uncorrected and SIR corrected results from the experiments with additions of amino-N, peptide-N and urea-N are shown in Fig. 3. All three sources of N were available for microorganisms when added as 0.45 mg $(g\ dw)^{-1}$, since the bioassay was able to assess an increased N availability fairly close to the value expected if the N sources were completely available (control + added amount of N). The 0.9 mg $(g\ dw)^{-1}$ additions were assessed less efficiently, as the obtained availability indices were all lower than expected.

Phosphorus availability

Oak forest floors tended to have high P availability and Norway spruce forest floors had the lowest P availability (Fig. 4). Only the uncorrected availability indices were significantly affected by tree species and site (both $P < 0.05$) (Fig. 4 and Table 2). The uncorrected availability indices were significantly higher for oak forest floors than for Douglas-fir, Sitka spruce and Norway spruce forest floors, and beech forest floors also had higher P availability than Norway spruce forest floors. Among sites, the uncorrected P availability was significantly higher at Frederiksborg than at Lindet. Uncorrected and SIR corrected P availability indices were both correlated with the corresponding N availability indices ($P < 0.001$, $r^2 = 0.74$ and $P < 0.05$, $r^2 = 0.40$, respectively).

Uncorrected P availability and SIR corrected P availability were closely correlated ($P < 0.001$, $r^2 = 0.83$). The results for oak at Frederiksborg differed more than for other samples (Fig. 4), and the correlation was improved ($P < 0.001$, $r^2 = 0.96$) when this forest floor was omitted. The SIR corrected P availability was on average 81 % (range 53-91%) of the uncorrected P availability (average 85% and range 72-91% without oak at Frederiksborg).

The two indices for available P were not correlated with total P concentrations in the forest floors (Table 3), but the indices tended to be negatively correlated with forest floor C/P

ratios (Table 1). However, the linear correlations were not quite significant ($P = 0.09$ for uncorrected P availability and $P = 0.14$ for SIR corrected P availability). The microbially available proportion of total P was much higher than for N (Table 3). Oak forest floors had a very large available proportion of P, whereas Norway spruce forest floors generally had the smallest available proportion of P across the sites. At Lindet, all tree species except beech tended to have smaller available proportions of P than at the other sites.

Basal respiration rate

Basal respiration rates were significantly different among sites ($P < 0.05$) (Table 2). Frederiksborg had the highest respiration rates, Lindet had the lowest rates, and rates at Ulborg were intermediate. Basal respiration rate did not differ significantly among tree species ($P = 0.06$), but oak tended to have higher rates than the other tree species. Basal respiration rate was positively related to uncorrected N availability and was also positively related to both P availability indices (Fig. 5). The variation in basal respiration rate was not significantly explained by KCl extractable N, total N concentrations, C/N ratios, total P concentrations, or C/P ratios.

DISCUSSION

Methodological considerations

Forest floors have a heterogeneous composition due to the variable origin of the organic material and the different stages of decomposition. At nutrient-rich sites like Frederiksborg, or in stands producing an easily decomposable litter, the forest floor may lack the H layer, while there may be H layers at more nutrient-poor sites, or in stands producing a slowly decomposing litter. The microbial species composition might also differ among forest floors, and their response to the bioassay may consequently be different as well. As discussed by Chapin *et al.* (1986), all plant species may not respond to the same extent in growth rate to increasing nutrient availability, i.e. nutrient supply and nutrient limitation are decoupled when species adapted to nutrient poor environments are used. It would be a problem for comparisons between different forest floors if the microbial populations in some forest floor responded more reluctantly to increased nutrient availability than in other forest floors. The large differences between SIR corrected and uncorrected N for oak and beech at Frederiksborg (Fig. 2) and between SIR corrected and uncorrected P for oak at Frederiksborg (Fig. 4) might indicate a different response pattern for forest floors of broadleaves at this site. Nordgren (1992) attributed large deviations between uncorrected and SIR corrected indices to differences between the nutrient content of newly formed microbial biomass and that of the native microbial biomass. Forest floors of broadleaves at the nutrient-rich site Frederiksborg may differ in microbial species composition, and the microbial response to nutrient limitation could be different as well. The availability indices were also less certain for these forest floors (Figs. 2 and 4), suggesting that the bioassay may not be equally suitable for all forest floor types.

The reliability of the bioassay also depends on the assumption that the amounts of added N or P used in the regressions are actually taken up by the microorganisms, i.e. that the measured response truly reflects the added amounts. KCl extraction of N before and after carrying out the bioassay for N on two forest floor samples (Norway spruce and Sitka spruce at Frederiksborg) showed that all added amounts of NH+,4 and also the originally KCl extractable N apparently were immobilized (results not shown). However, the added NH+,4 may not only have been microbially immobilized. For instance, NH+,4 might have been immobilized through reactions with quinones, polyphenols or other recalcitrant organic substances thereby becoming unavailable for microorganisms (Kelley and Stevenson, 1995). This would lead to overestimated values for microbially available N. As forest floor material from different sites and tree species could be expected to differ in organic constituents (Johansson, 1995), variable NH4,+-fixation might obscure tree species or site differences.

Addition of organic N sources (Fig. 3) revealed that both the uncorrected and the SIR corrected index assessed the low amount of added organic N fairly well. The less exact estimates of larger amounts of added N may be caused by limitations in the bioassay setup, i.e. that the bioassay is unable to assess N pools as adequately in this availability regime if other limiting nutrients are not supplied in greater amounts. However, the results indicate that the bioassay was able to estimate N availability within the low addition regime, and that simple organic N sources were included in the available pool of N. This may also explain the lack of correlation between KCl extractable N and bioassay N. Binkley and Vitousek (1989) reported results for bioassay seedling uptake of N versus KCl extraction, which indicated that their bioassay detected two times the amount detected by KCl extraction and 2% of total N. However, microorganisms might be capable of extracting organic N more efficiently than plant roots. The available proportions of the total N concentration (Table 3) were also higher than the proportion available for bioassay seedling uptake in the study by Binkley and Vitousek (1989). Scheu and Parkinson (1995) also found a poor relationship between KCl extractable N and the respiratory response to N addition, and concluded that KCl extractions probably do not provide a proper estimate of the N pool available to microorganisms.

Compared with the available percentages of total N, the available percentages of total P were remarkably high (~100%) in some of the forest floors (Table 3) indicating that organic P sources were fully available in some forest floors. Available proportions larger than 100% could be due to slightly lower P concentrations in the pooled forest floor material used for total analysis than in the FH material. Some fungi are able to extract organic P selectively due to production of specific enzymes (Häussling and Marschner, 1989; Dighton, 1991). If saprophytic fungi with such properties were among the responding organisms in the bioassay, it might explain the high availability of P. However, P availability was high compared with the P availability reported by Nordgren (1992) for a North Scandinavian coniferous forest (0.17 mg g^{-1}). A similar P availability (0.15 mg g^{-1} corresponding to about 30% of total P) was found in H layer forest floor material in another Danish Norway spruce stand (L. Vesterdal,

unpublished data), indicating that lower P availability may also be found in Danish forest floors. Higher available proportions of total P than of total N may be due to condensation reactions between amino-N and polyphenols which have been reported from several studies (Kelley and Stevenson, 1995). Nitrogen availability might therefore depend on the concentration of organic compounds as tannins, polyphenols or lignin in the litter while organic P may be more available due to less immobilization in organic forms unavailable to microorganisms.

Basal respiration rate and availability of N and P

Basal respiration rates in the forest floor samples were positively correlated with the availability indices for both N and P (Fig. 5). The microbial N and P availability indices were correlated, so microbial activity may have been limited by either available N or P or both within the range of soil types and tree species investigated. Thus, the bioassay appeared to provide relevant information about the nutritional conditions determining microbial activity in forest floors. These nutritional conditions might rather be determined by the forms of N and P than by the total amounts present in forest floors. However, positive correlations between microbial activity and more commonly applied N and P indices were reported from other studies. Tewary *et al.* (1982) and Jorgensen and Wells (1973) found that basal respiration rate was positively correlated with total N in forest floors. Jorgensen and Wells (1973) also carried out KCl extractions and total P determinations on the forest floor material, but basal respiration rates were only weakly correlated with these indices.

Differences among tree species

Differences among the tree species in litterfall N and P concentrations may be one of the factors leading to variable forest floor N and P availability (Table 2, Figs. 2 and 4). In forest floor bioassay studies, Prescott *et al.* (1992, 1993) found that total concentrations of N and P in litter and KCl extractable N and Bray extractable P in forest floors of different tree species were related to plant growth and plant N and P uptake. Higher microbial N and P availability in the oak forest floors may similarly be a result of higher N and P concentrations in oak litter than in litter of the other tree species. At Lindet and Ulborg, oak forest floors correspondingly had the lowest C/N and C/P ratios, but forest floor C/N and C/P ratios at Frederiksborg did not lend support to the differences among tree species in N and P availability (Table 1).

Scheu and Parkinson (1995) studied microbial N and P status in forest floors of two tree species and reported that the microbial respiratory response to N and P additions corresponded with C/N ratios and Bray-extractable P, respectively. In this study, microbially available N and P did not correspond with the total concentrations, and correlations with C/N and C/P ratios were not significant. Other factors might therefore control nutrient availability in forest floors of different tree species. Some of the compounds containing N and P, e.g. proteins, may be embedded in a matrix of recalcitrant lignin, which prevents microorganisms

from getting access to these N and P sources (Berg, 1986). Tannins in litter may also inhibit N availability through immobilization of N. As the lignin and tannin concentrations in litter varies among tree species (Johansson, 1995; Northup *et al.*, 1995), these properties may be important for N and P availability in forest floors. Foliage litter of Norway spruce and beech have fairly high lignin concentrations (Staaf, 1980; Johansson, 1995), and Kuiters and Denneman (1987) reported that polyphenol concentrations were higher in the forest floor and soil under Norway spruce and beech than under oak. The differences among tree species in microbial N and P availability in forest floors might therefore rather be caused by different microbial access to organic N and P sources than by different total amounts of N and P.

Differences among sites

Beside tree species, soil nutrient status is recognized as a significant factor influencing the nutrient concentrations in litter and in turn the nutrient concentrations in the forest floor (Boerner, 1984; Raulund-Rasmussen and Vejre, 1995). The soil N and P status at the three sites could therefore have affected forest floor N and P availability among the sites. Forest floor C/N ratios were lowest at Lindet and Ulborg (Table 1), suggesting that N availability might be higher at these sites. However, sites did not differ significantly in microbial N availability, and Fig. 2 shows that differences among sites were evident only for some of the tree species (oak, beech, Douglas-fir). This suggests that sites affected N availability more in some tree species than in others. As the N status of a site does not depend directly on soil parent material, other site specific factors may also be important for microbial N availability. Atmospheric deposition of N has increased during the last decades, and in Denmark deposition gradients may exist both locally and regionally. The throughfall flux of $NH_{+,4}$-N in Sitka spruce was significantly largest at Lindet due to high emissions in this region, intermediate at Ulborg and lowest at Frederiksborg (Pedersen, 1993). Forest floors correspondingly had low C/N ratios and high concentrations of total N at Lindet (Tables 1 and 3). In spite of this, microbial N availability was more likely to be lower at Lindet than at the other two sites. Also among sites, the amount of specific organic compounds in the litter could be more important for microbial nutrient availability than just ample amounts of total N. Soil type dependent differences in the lignin and tannin concentrations in litter (Northup *et al.*, 1995; Sanger, 1996) may influence the N availability in forest floors of a given tree species at different sites.

Phosphorus availability was expected to be more related to soil parent material than N availability. The trend in P availability tended to correspond with C/P ratios in the forest floor and with soil P. Phosphorus availability was lower at Ulborg and Lindet where soils were most poor in P (Table 1). However, availability of P was very high in the beech forest floor from Lindet and differences in microbial P availability were small compared with the differences in soil P.

Conclusions

The bioassay assessed simple organic N compounds fairly well when added in small amounts (0.45 mg g^{-1}), whereas larger amounts were assessed less exactly. Microbial availability of N and P was not significantly related to total N and P concentrations or to C/N and C/P ratios, and N availability was not related to KCl extractable N. The available proportion of total P was much higher than the available proportion of total N. Potential N and P availability differed among forest floors of the five tree species. Oak forest floors had higher microbial N availability than forest floors of the other tree species, and P availability was highest in oak forest floors and lowest in Norway spruce forest floors. Sites differed only slightly in forest floor P availability, but the site most rich in mineral soil P also had the highest microbial P availability. Basal respiration rate was positively related to microbial N and P availability. Influence of tree species and sites may partly be due to differences in N and P status of litter and soils, but microbial N and P availability in forest floors may also depend on other litter quality variables related to microbial access to nutrients in organic forms.

Acknowledgements—This study was financially supported by The European Commission. I would like to thank Camilla Hoppe for carrying out most of the sample preparations in the laboratory and The Danish Forest and Landscape Research Institute for kindly allowing me to use the tree species trial.

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Table 1. Forest floor properties for the stands and mineral soil properties for the three sites

Site and tree species	Forest floor[a]				Mineral soil 0-30 cm[b]		
	C	pH	C/N	C/P	pH	N	P
	Mg ha^{-1}	($CaCl_2$)			($CaCl_2$)	mg g^{-1}	mg kg^{-1}
Frederiksborg					4.9	0.93	126
Norway spruce	4.54	5.0	27.3	378			
Beech	2.92	5.1	28.9	463			
Sitka spruce	7.21	4.1	27.4	519			
Douglas fir	2.34	4.4	27.5	312			
Oak	1.51	4.3	27.5	472			
Ulborg					3.8	2.03	16
Norway spruce	19.78	3.5	24.8	553			
Beech	19.26	3.8	22.2	463			
Sitka spruce	20.69	3.5	25.3	621			
Douglas fir	15.92	3.7	23.2	569			
Oak	6.10	3.8	20.3	361			
Lindet					3.0	0.90	16
Norway spruce	20.79	3.3	23.4	589			
Beech	15.20	3.7	22.6	603			
Sitka spruce	16.56	3.7	23.1	552			
Douglas fir	11.43	3.5	21.2	577			
Oak	8.19	4.0	20.4	515			

[a] Vesterdal and Raulund-Rasmussen (submitted manuscript, 1997).

[b] Soil horizon-weighted data based on Raulund-Rasmussen (1993).

Table 2. Microbial availability of N and P, and basal respiration (±1 SEM) in forest floors. Tree species means (n = 3) and site means (n = 5) followed by the same superscript letter or no letter are not significantly different ($P > 0.05$) based on ANOVA and Duncan's multiple range test.

	Nitrogen		Phosphorus		Basal respiration
	Uncorr.	SIR corr.	Uncorr.	SIR corr.	
	mg g^{-1}		mg g^{-1}		mg CO_2 g^{-1} h^{-1}
Tree species					
Oak	2.40 (0.53)^{a}	1.57 (0.33)^{a}	0.91 (0.19)^{a}	0.66 (0.06)	0.25 (0.03)
Douglas fir	1.35 (0.18)^{b}	1.02 (0.10)^{ab}	0.61 (0.14)^{ab}	0.49 (0.12)	0.11 (0.02)
Beech	1.35 (0.13)^{b}	0.86 (0.09)^{b}	0.57 (0.07)^{bc}	0.46 (0.08)	0.15 (0.04)
Sitka spruce	1.19 (0.09)^{b}	0.83 (0.15)^{b}	0.47 (0.09)^{bc}	0.39 (0.06)	0.16 (0.07)
Norway spruce	1.07 (0.02)^{b}	0.79 (0.05)^{b}	0.36 (0.06)^{c}	0.31 (0.05)	0.12 (0.03)
Sites					
Frederiksborg	1.57 (0.43)	0.87 (0.16)	0.75 (0.14)^{a}	0.53 (0.06)	0.22 (0.04)^{a}
Ulborg	1.50 (0.26)	1.11 (0.28)	0.55 (0.09)^{ab}	0.46 (0.08)	0.15 (0.03)^{ab}
Lindet	1.19 (0.10)	0.97 (0.04)	0.46 (0.10)^{b}	0.37 (0.09)	0.11 (0.03)^{b}

Table 3. Some fractions of N and P in the studied forest floors, and the percentages of total concentrations determined on FH material by KCl extraction and in the bioassay.

	Total N[a]	KCl-N		Available N		Total P[a]	Available P	
				uncorr.	SIR		uncorr.	SIR
	mg g^{-1}	mg g^{-1}	%	%		mg g^{-1}	%	
Frederiksborg								
Norway spruce	12.8	0.38	3.0	9	6	0.93	52	45
Beech	13.0	0.08	0.6	12	6	0.81	72	52
Sitka spruce	14.9	0.27	1.8	7	4	0.78	83	65
Douglas fir	9.6	0.21	2.2	15	10	0.83	90	76
Oak	17.1	0.02	0.1	20	9	1.00	127	73
Ulborg								
Norway spruce	13.9	0.49	3.5	8	5	0.63	52	44
Beech	12.8	0.25	2.0	9	6	0.61	85	70
Sitka spruce	16.6	0.60	3.6	8	7	0.67	64	57
Douglas fir	16.8	0.67	4.0	10	7	0.69	99	86
Oak	13.6	1.13	8.3	19	16	0.76	107	96
Lindet								
Norway spruce	18.9	0.20	1.0	5	5	0.75	37	33
Beech	17.9	0.34	1.9	7	6	0.67	110	100
Sitka spruce	20.0	0.34	1.7	6	5	0.84	39	36
Douglas fir	20.1	0.36	1.8	5	5	0.74	39	35
Oak	20.3	0.36	1.8	8	6	0.81	79	68

[a] applies to the whole forest floor.

N: dry combustion (Leco CHN analyzer)

P: digestion in conc. HNO_3 followed by flow injection analysis.

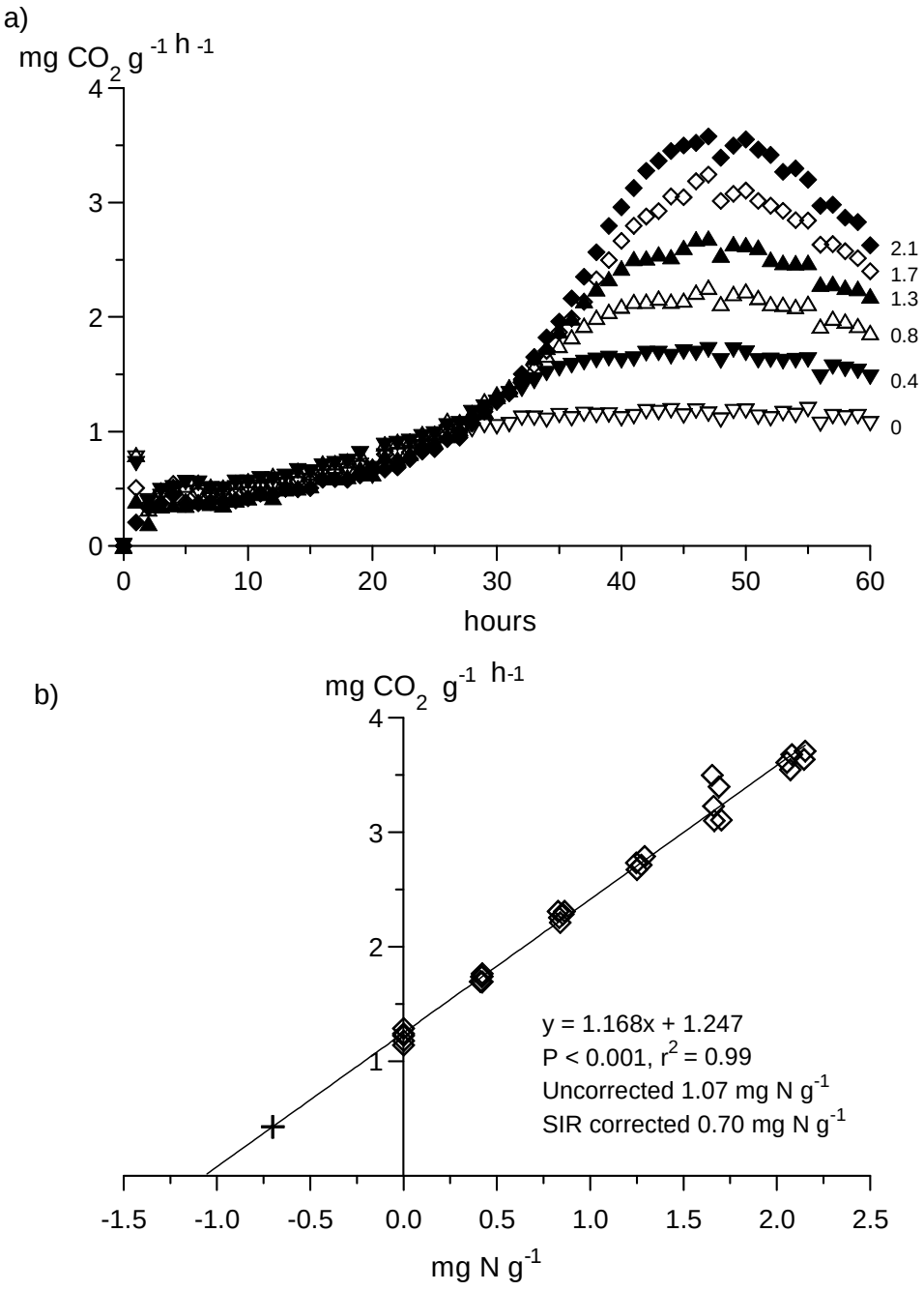

Fig. 1. Determination of potential microbial N availability in forest floor material from Norway spruce at Ulborg. a) average respiration rates (n = 5) resulting from different additions of N (mg (g dw)$^{-1}$) together with glucose and P in excess. Substrate induced repiration rate (SIR) is the stable respiration rate attained immediately after start of the experiment. b) regression based on the obtained limited respiration rates. SIR is indicated by +.

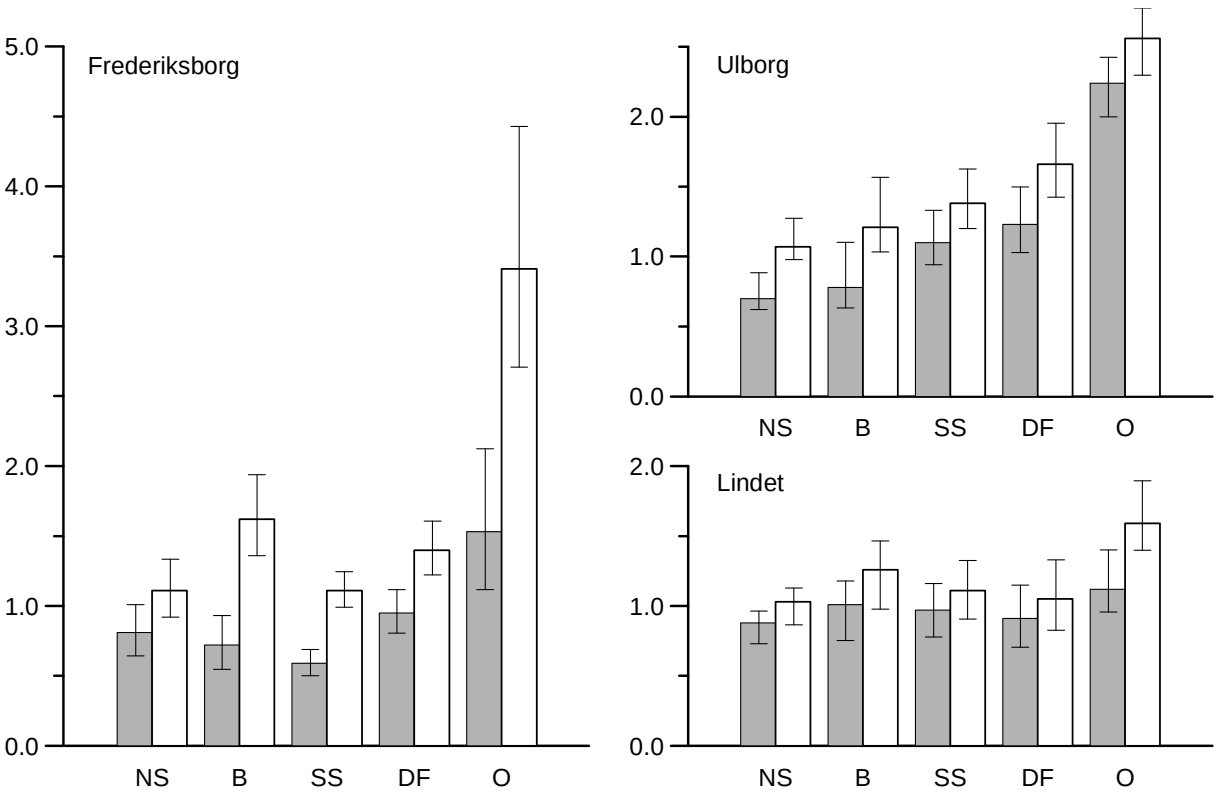

Fig. 2. Potential microbial N availability (mg g^{-1}). Shaded bars are SIR corrected N availability. Error bars are 95% confidence intervals. Tree species: NS, Norway spruce; B, beech; SS, Sitka spruce; DF, Douglas-fir; O, oak.

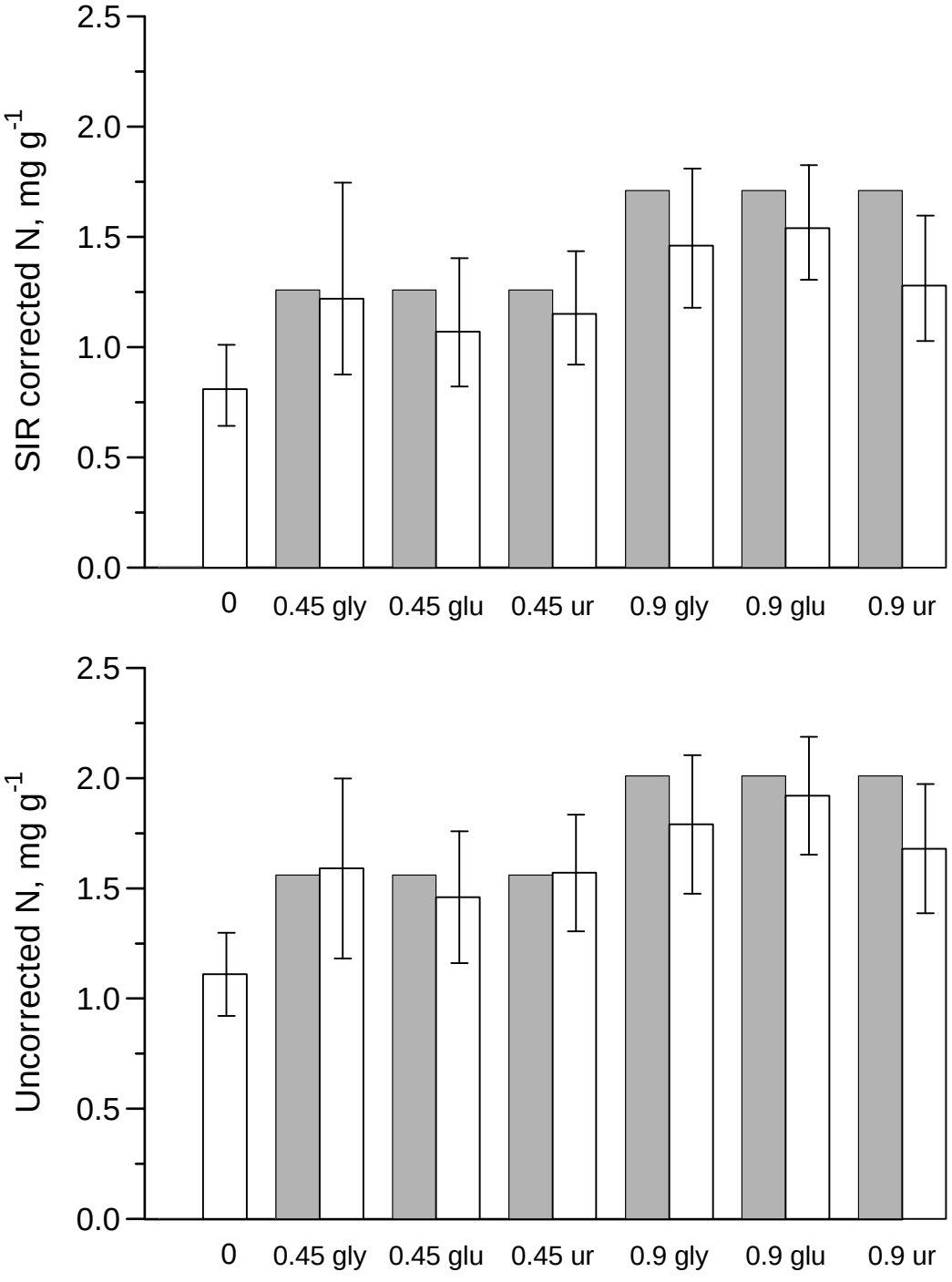

Fig. 3. SIR corrected and uncorrected microbially available N found before (0) and after addition of 0.45 or 0.9 mg g^{-1} dw of glycine-N (gly), glutathione-N (glu), or urea-N (ur) to forest floor material. Shaded bars indicate the theoretical availability after addition of organic N sources. Thin bars are 95% confidence intervals.

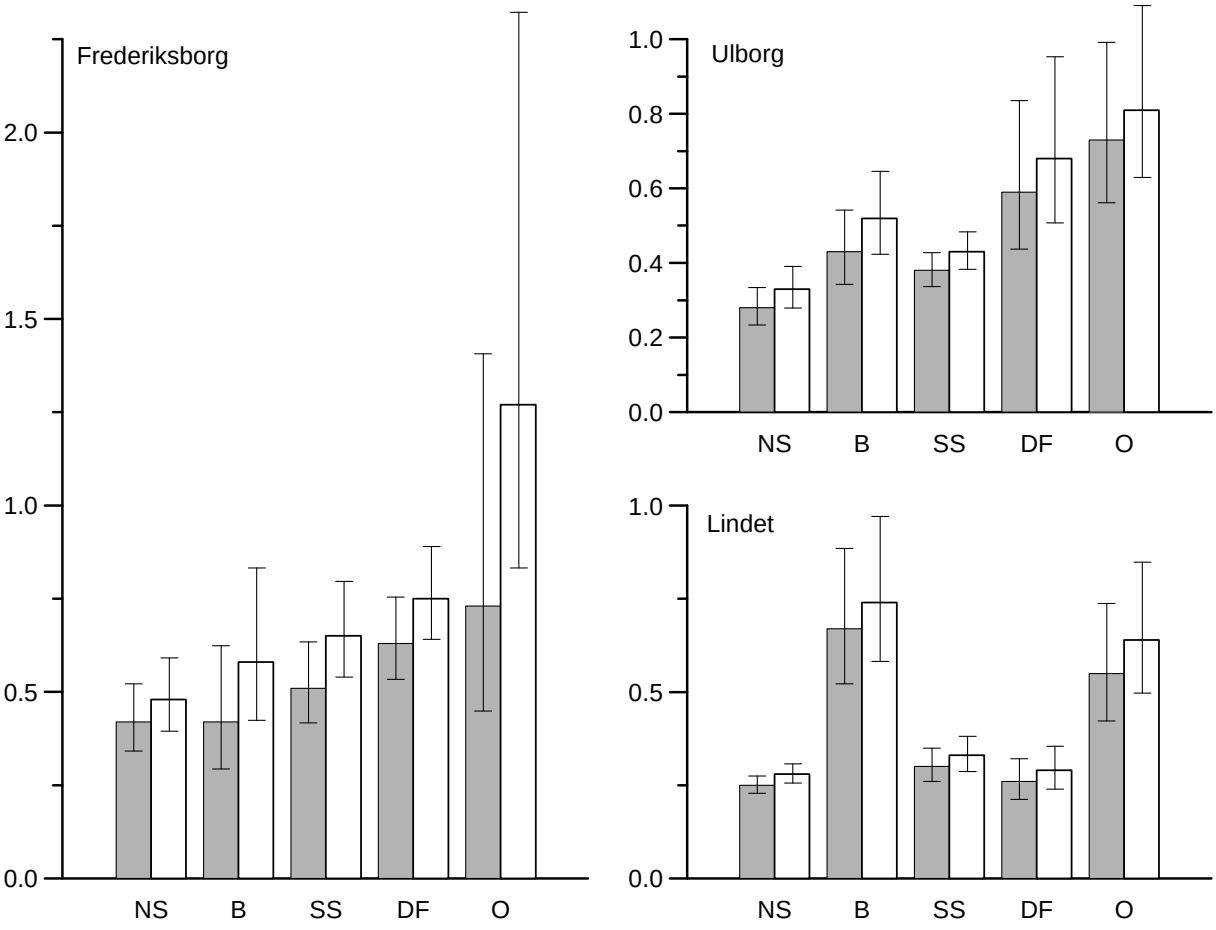

Fig. 4. Potential microbial P availability (mg g^{-1}). Shaded bars are SIR corrected P availability. Error bars are 95% confidence intervals. Tree species legend as in Fig. 2.

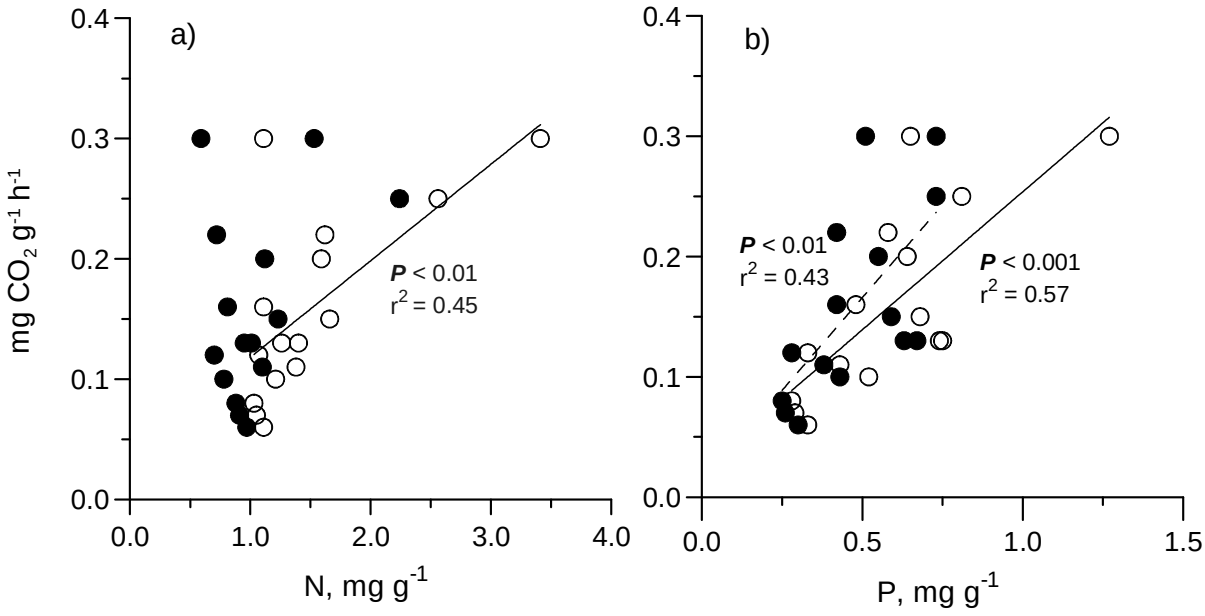

Fig. 5. a) Correlations between basal respiration rate and N availability in the forest floor. b) Correlations between basal respiration rate and P availability in the forest floor. ❍ and ——— , uncorrected availability; ● and -------- , SIR corrected availability.